HARVARD UNIVERSITY

Library of the
Museum of
Comparative Zoology

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOLUME 94 1982 QUARTERLY

EDITOR: JON C. BARLOW
ASSOCIATE EDITOR: MARGARET L. MAY
REVIEW EDITOR: ROBERT RAIKOW
COLOR PLATE EDITOR: WILLIAM A. LUNK
ASSISTANT EDITORS: KEITH L. BILDSTEIN
GARY BORTOLOTTI
NANCY FLOOD
SENIOR EDITORIAL ASSISTANTS: JANET T. MANNONE
RICHARD R. SNELL
EDITORIAL ASSISTANTS: C. DAVISON ANKNEY
PETER M. FETTEROLF
JAMES D. RISING

President—Abbot S. Gaunt, Department of Zoology, Ohio State University, Columbus, Ohio 43210.

First Vice-President—Jerome A. Jackson, Department of Biological Sciences, P.O. Drawer Z, Mississippi State University, Mississippi State, Mississippi 39762.

Second Vice-President—Clait E. Braun, Wildlife Research Center, 317 West Prospect St., Fort Collins, Colorado 80526.

Editor—Jon C. Barlow, Department of Ornithology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, M5S 2C6 Canada.

Secretary—Curtis S. Adkisson, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.

Treasurer—Robert D. Burns, Department of Biology, Kenyon College, Gambier, Ohio 43022.

Elected Council Members—Mary H. Clench (term expires 1983); Helen Lapham (term expires 1984); Anthony J. Erskine (term expires 1985).

DATES OF ISSUE OF VOLUME 94
OF THE WILSON BULLETIN

NO. 1—22 APRIL 1982
NO. 2—24 JUNE 1982
NO. 3—28 SEPTEMBER 1982
NO. 4—31 JANUARY 1983

CONTENTS OF VOLUME 94

NUMBER 1

THE STATUS OF THE AVIFAUNA OF THE REVILLAGIGEDO ISLANDS, MEXICO
Joseph R. Jehl, Jr., and Kenneth C. Parkes 1

AVIAN POPULATION FLUCTUATIONS DURING DROUGHT CONDITIONS IN PUERTO RICO
John Faaborg 20

NEST-SITES AND HABITAT OF RED-SHOULDERED AND RED-TAILED HAWKS IN IOWA
James C. Bednarz and James J. Dinsmore 31

BREEDING BIOLOGY AND DIET OF THE FERRUGINOUS HAWK IN SOUTH DAKOTA
Charles L. Blair and Frank Schitoskey, Jr. 46

IMPLICATIONS OF CONSTRUCTION OF A FLOOD CONTROL PROJECT UPON BALD EAGLE NESTING ACTIVITY ---------- *Anne E. Shapiro, Frank Montalbano, III, and Doris Mager* 55

FUNGI AND RED-COCKADED WOODPECKER CAVITY TREES
Richard N. Conner and Brian A. Locke 64

GENERAL NOTES

THE HUMEROULNAR PULLEY AND ITS EVOLUTION IN HUMMINGBIRDS
Gregory D. Bentz and Richard L. Zusi 71

RELATIONSHIPS OF ENVIRONMENTAL FACTORS TO ONSET OF AUTUMN MORNING VOCALIZATIONS IN AN OZARK COMMUNITY -------- *Richard M. Zammuto and Douglas James* 74

POSSIBLE COURTSHIP BEHAVIOR BY SNOWY OWLS IN WINTER
Peter C. Boxall and M. Ross Lein 79

DIFFERENTIAL HUNTING SUCCESS IN A GROUP OF SHORT-EARED OWLS
Thomas G. Marr and Douglas W. McWhirter 82

OBSERVATIONS AT A LAUGHING FALCON NEST *Mark B. Robbins and David A. Wiedenfeld* 83

EVIDENCE OF BALD EAGLES FEEDING ON FRESHWATER MUSSELS
Teryl G. Grubb and Michael A. Coffey 84

KILLDEERS FEEDING ON FROGS ---------- *Bette J. Schardien and Jerome A. Jackson* 85

POSSIBLE USE OF LEGS AS DISSIPATORS OF HEAT IN FLYING CLIFF SWALLOWS
Robert W. Butler 87

ACTIVE ANTING BY THE YELLOW-SHOULDERED BLACKBIRD
William Post and Micou M. Browne 89

COMPETITION BETWEEN RED-WINGED BLACKBIRDS AND COMMON GRACKLES
Sarah Lenington and Rose Scola 90

INCIDENCE OF BROWN-HEADED COWBIRD PARASITISM ON RED-WINGED BLACKBIRDS
George M. Linz and Susan B. Bolin 93

WESTERN KINGBIRD NESTS IN ABANDONED WOODPECKER CAVITY -- *Benedict C. Pinkowski* 95

PIRACY BY A GREAT BLACK-BACKED GULL ON A SHARK ---------- *Thomas W. French* 96

ORNITHOLOGICAL LITERATURE ---------- 97

ORNITHOLOGICAL NEWS ---------- 104

NUMBER 2

A NEW SPECIES OF ANTPITTA (*GRALLARIA*) FROM NORTHERN PERU
Thomas S. Schulenberg and Morris D. Williams 105

THE RELATIONSHIPS OF THE VIREOS (VIREONINAE) AS INDICATED BY DNA-DNA HYBRIDIZATION ---------- *Charles G. Sibley and Jon E. Ahlquist* 114

VEGETATION RELATIONSHIPS AND FOOD OF SAGE SPARROWS WINTERING IN HONEY MESQUITE HABITAT ---------- *Julie K. Meents, Bertin W. Anderson and Robert D. Ohmart* 129

ECOLOGICAL RELEASE AND ECOLOGICAL FLEXIBILITY IN HABITAT USE AND FORAGING OF AN INSULAR AVIFAUNA ---------- *Monique I. Vassallo and Jake C. Rice* 139

AVIAN NEST DENSITIES AND NEST-SITE SELECTION IN FARMSTEAD SHELTERBELTS
Richard H. Yahner 156

THE INFLUENCE OF SEASONALITY AND SELECTED WEATHER VARIABLES ON AUTUMN MIGRATION OF THREE SPECIES OF HAWKS THROUGH THE CENTRAL APPALACHIANS
Kimberly Titus and James A. Mosher 176

RADIONUCLIDES IN MOURNING DOVES NEAR A NUCLEAR FACILITY COMPLEX IN SOUTHEASTERN IDAHO ---------- *O. Doyle Markham and Douglas K. Halford* 185

GENERAL NOTES

GREAT BLUE HERON EGGSHELL THICKNESS AT OREGON ESTUARIES ------ *Range D. Bayer* 198

NESTING PHENOLOGY OF THE DOUBLE-CRESTED CORMORANT
James A. Kushlan and Linda C. McEwan 201

REPLACEMENT NESTING AND POLYANDRY IN THE WATTLED JACANA ---- *David R. Osborne* 206

HABITAT OF BACHMAN'S SPARROWS BREEDING ON MISSOURI GLADES
Kimberly I. Hardin, Thomas S. Baskett and Keith E. Evans 208

A DOUBLE-BROODED EASTERN KINGBIRD ------ *Peter J. Blancher and Raleigh J. Robertson* 212

MALE COOPER'S HAWK BREEDS IN JUVENAL PLUMAGE
Robert N. Rosenfield and Jonathan Wilde 213

UNUSUAL FEEDING BEHAVIOR BY A POPULATION OF BLACK VULTURES
Donald J. Elias and Danilo Valencia G. 214

CLAPPER RAIL PREYS ON SAVANNAH SPARROW
Paul D. Jorgensen and Howard L. Ferguson 215

COMMENSAL FEEDING OF LITTLE BLUE HERONS WITH MANATEES
Michael D. Scott and James A. Powell 215

COMPARISON OF THE NEST-SITE DISTRACTION DISPLAYS OF BLACK-CAPPED CHICKADEE AND WHITE-BREASTED NUTHATCH ---------- *Charles A. Long* 216

A REVIEW OF HYBRIDIZATION BETWEEN *SIALIA SIALIS* AND *S. CURRUCOIDES*
Richard C. Rounds and Hugh L. Munro 219

INTERSPECIFIC PLUMAGE SIMILARITY: THE MOCKINGBIRD AND LOGGERHEAD SHRIKE
Robert W. Ficken and Millicent S. Ficken 223

HEAD WIND PROMOTES SKIMMING IN LAUGHING GULLS
Jack P. Hailman and Jonathan R. Reed 223

A LAMP-BOOTH FOR LABORATORY USE ---------- *Colleen Nelson* 225

ORNITHOLOGICAL LITERATURE ---------- 230

ORNITHOLOGICAL NEWS ---------- 239

NUMBER 3

SYSTEMATIC RELATIONSHIPS AND ZOOGEOGRAPHY OF THE WHITE-WINGED GUAN (*PENELOPE ALBIPENNIS*) AND RELATED FORMS ---------- *J. William Eley* 241

ON THE MATING SYSTEM OF BROWN-HEADED COWBIRDS ---- *C. Davison Ankney and D. M. Scott* 260

KLEPTOPARASITISM BY SOUTH POLAR SKUAS ON BLUE-EYED SHAGS IN ANTARCTICA
Stephen J. Maxson and Neil P. Bernstein 269

INTRASPECIFIC FOOD ROBBING IN GLAUCOUS-WINGED GULLS ------ *Elizabeth Drexler Rockwell* 282

EFFECT OF FOREST STRUCTURE ON AMERICAN REDSTART FORAGING BEHAVIOR
George E. Seidel and Robert C. Whitmore 289

FACTORS INFLUENCING WINTER DISTRIBUTION AND ABUNDANCE OF TOWNSEND'S SOLITAIRE
Carl E. Bock 297

MIGRATION PATTERNS OF RED AND NORTHERN PHALAROPES IN SOUTHWEST DAVIS STRAIT AND IN THE NORTHERN LABRADOR SEA
Craig D. Orr, Richard M. P. Ward, Norman A. Williams, and R. G. B. Brown 303

RECRUITMENT AND SOCIALLY-SPECIFIC FLOCKING TENDENCIES OF EASTERN SANDHILL CRANES
James R. Lovvorn and Charles M. Kirkpatrick 313

EFFECTS OF CONTEXTUAL INFORMATION ON BEHAVIOR OF *CALIDRIS* SANDPIPERS FOLLOWING ALARM CALLS ---------- *Daniel W. Leger and Jami L. Nelson* 322

NEST-SITE SELECTION BY CAVITY-NESTING BIRDS OF RIPARIAN HABITATS IN IOWA
Dean F. Stauffer and Louis B. Best 329

NESTS, TERRITORIES, AND REPRODUCTION OF SEDGE WRENS (*CISTOTHORUS PLATENSIS*)
Jeffrey T. Burns 338

GENERAL NOTES

NOTES ON MIGRANTS WINTERING AT MONTEVERDE, COSTA RICA
Elliot J. Tramer and Thomas R. Kemp 350

DECLINE OF THE ROADRUNNER IN MISSOURI ------ *Douglas J. Norris and William H. Elder* 354

THE OCCURRENCE AND BEHAVIOR OF NON-BREEDING HORNED PUFFINS AT BLACK GUILLEMOT COLONIES IN NORTHERN ALASKA ---------- *George J. Divoky* 356

BODY TEMPERATURE AND GROWTH OF BONIN PETREL CHICKS
Ted N. Pettit, Gilbert S. Grant, and G. Causey Whittow 358

PROLONGED INCUBATION BEHAVIOR IN COMMON LOONS ---------- *Scott Sutcliffe* 361

BARN SWALLOW FLEDGLING SUCCESSFULLY ELICITS FEEDING AT A NON-PARENTAL NEST
Gregory Ball 362

COWBIRD CONTROL AND ITS EFFECT ON KIRTLAND'S WARBLER REPRODUCTIVE SUCCESS
Sean T. Kelly and Michael E. DeCapita 363

UNUSUAL NEST SANITATION BY A BROAD-WINGED HAWK
Robert N. Rosenfield, Adam J. Rosenfield, and Michael W. Gratson 365

FIRST RECORD OF A BALD EAGLE NEST IN WEST VIRGINIA
Maurice N. LeFranc, Jr., Thomas A. Pierson, and Michael G. May 366

OSPREY SPREADS WINGS AFTER FISHING ---------- *A. M. Elowson-Haley* 366

ROUGH-WINGED SWALLOWS SCAVENGING ADULT MIDGES ---------- *Spencer G. Sealy* 368

DIET OF GLAUCOUS GULLS IN WESTERN ALASKA ---------- *Carl Strang* 369

VOCAL BEHAVIOR OF THE NORTHERN ORIOLE ---------- *L. David Beletsky* 372

DOCUMENTATION AND STATUS OF CORY'S SHEARWATER IN THE WESTERN GULF OF MEXICO ---------- *Warren Pulich, Jr.* 381

ORNITHOLOGICAL LITERATURE ---------- 386

LIST OF BOOKS IN THE JOSSELYN VAN TYNE MEMORIAL LIBRARY, THE WILSON ORNITHOLOGICAL SOCIETY ---------- 393

PRESIDENT'S MESSAGE ---------- 430

ORNITHOLOGICAL NEWS ---------- 259, 432

NUMBER 4

THE BIOLOGY OF *TORREORNIS INEXPECTATA* I. A COMPARISON OF VOCALIZATIONS IN *T. I. INEXPECTATA* AND *T. I. SIGMANI* ---------- *Eugene S. Morton and Hiram J. Gonzalez Alonso* 433

THE BEHAVIOR OF SCALE-BACKED ANTIBIRDS ---------- *Edwin O. Willis* 447

CENSUSES AND BREEDING OBSERVATIONS OF THE BIRDS ON KOHALA MOUNTAIN, HAWAII *Charles van Riper, III* 463

OBSERVATIONS OF SOME UNUSUAL RAINFOREST AND MARSH BIRDS IN SOUTHEASTERN PERU ---------- *Theodore A. Parker, III* 477

MIGRATION AND SUMMER DISTRIBUTION OF LESSER SNOW GEESE IN INTERIOR KEEWATIN *Peter L. McLaren and Margaret A. McLaren* 494

ECOLOGICAL SEPARATION OF GREBES AND COOTS: INTERFERENCE COMPETITION OR MICROHABITAT SELECTION? ---------- *Thomas D. Nudds* 505

ROLE SPECIALIZATION IN THE PARENTAL AND TERRITORIAL BEHAVIOR OF THE KILLDEER *John T. Mundahl* 515

BIOLOGY AND BEHAVIOR OF BREEDING PIPING PLOVERS ---------- *Winifred E. Cairns* 531

GENERAL NOTES

COMPARISON OF VARIABLE CIRCULAR-PLOT AND SPOT-MAP METHODS IN DESERT RIPARIAN AND SCRUB HABITATS ---------- *Robert C. Szaro and Martin D. Jakle* 546

USE OF PRAIRIE WETLANDS BY SELECTED BIRD SPECIES IN SOUTH DAKOTA *Michael J. Weber, Paul A. Vohs, Jr., and Lester D. Flake* 550

SEXING SAW-WHET OWLS BY WING CHORD ---------- *Helmut C. Mueller* 554

COMMENTS ON SEXING SAW-WHET OWLS BY WING CHORD *Martin H. Edwards, Ron D. Weir, and Robert B. Stewart* 555

USE OF TWO HABITATS RELATED TO CHANGES IN PREY AVAILABILITY IN A POPULATION OF OSPREYS IN NORTHEASTERN NOVA SCOTIA *Ian Jamieson, Norman R. Seymour, and Robert P. Bancroft* 557

NEST PROVISIONING BEHAVIOR BY A MALE NORTHERN HARRIER ON THE DEATH OF HIS MATE ---------- *Steven P. Thompson and John E. Cornely* 564

NOTES ON THE HUNTING BEHAVIOR AND DIET OF THE CRESTED CARACARA IN NORTHEASTERN CHIAPAS AND TABASCO, MEXICO *David Whitacre, Devora Ukrain, and Gary Falxa* 565

FLORIDA RED-SHOULDERED HAWK ROBS AMERICAN CROWS ---------- *Lawrence Kilham* 566

FEEDING BEHAVIORS AND EFFICIENCIES OF COMMON AND FORSTER'S TERNS *J. Michael Reed, Herbert E. Hays, and David A. Zegers* 567

CLUTCH-SIZE AND PREFLEDGING SURVIVAL IN RED-WINGED BLACKBIRDS AT WILLIAMSTOWN LAKE, NEW BRUNSWICK ---------- *Michael D. Rigby* 569

GROWTH, DIET, AND MORTALITY OF NESTLING GREAT BLUE HERONS ---------- *T. E. Quinney* 571

DOWNY WOODPECKER SEXES SELECT DIFFERENT CAVITY SITES: AN EXPERIMENT USING ARTIFICIAL SNAGS ---------- *Thomas C. Grubb, Jr.* 577

A NEST OF THE PALE-BILLED ANTPITTA (*GRALLARIA CARRIKERI*) WITH COMPARATIVE REMARKS ON ANTPITTA NESTS ---------- *David A. Wiedenfeld* 582

INTERSPECIFIC NEST USE BY ARIDLAND BIRDS ---------- *Deborah M. Finch* 582

AN APPARENT INSTANCE OF COMMUNAL NESTING BY AMERICAN OYSTER CATCHERS *Brian R. Chapman* 584

SONG SPARROW PAIR RAISE FOUR BROODS IN ONE YEAR ---------- *James N. M. Smith* 584

POST-COPULATORY DISPLAY IN THE LARK BUNTING AND OTHER SPECIES *Robert W. Nero* 585

RESPONSES OF BLACK-CAPPED CHICKADEES TO MIRRORS *Ellen J. Censky and Millicent S. Ficken* 590

TOOL USE BY GREEN JAYS ---- *Douglas C. Gayou* 593
A FLIGHT-SONG DISPLAY OF WHITE-THROATED MANAKIN ---- *Thomas H. Davis* 594
NOTES ON THE AGONISTIC BEHAVIOR OF COMMON MURRES
Shane P. Mahoney and William Threlfall 595
RECORDS OF REDHEAD × CANVASBACK HYBRIDS ---- *G. M. Haramis* 599
HIGH MORTALITY OF CEDAR WAXWINGS ASSOCIATED WITH HIGHWAY PLANTINGS
Robert C. Dowler and Gustav A. Swanson 602

ORNITHOLOGICAL LITERATURE ---- 604

PROCEEDINGS OF THE SIXTY-THIRD ANNUAL MEETING ---- 612

INDEX ---- 624

WIL
8424
.a

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 94, NO. 1 MARCH 1982 PAGES 1–104

MUS. COMP. ZOOL.
LIBRARY
MAY 4 1982
HARVARD
UNIVERSITY

THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

President—Abbot S. Gaunt, Department of Zoology, Ohio State University, Columbus, Ohio 43210.

First Vice-President—Jerome A. Jackson, Department of Biological Sciences, P.O. Drawer Z, Mississippi State University, Mississippi State, Mississippi 39762.

Second Vice-President—Clait E. Braun, Wildlife Research Center, 317 West Prospect St., Fort Collins, Colorado 80526

Editor—Jon C. Barlow, Department of Ornithology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6.

Secretary—Curtis S. Adkisson, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.

Treasurer—Robert D. Burns, Department of Biology, Kenyon College, Gambier, Ohio 43022.

Elected Council Members—Richard C. Banks (term expires 1982); Mary H. Clench (term expires 1983); Helen Lapham (term expires 1984).

Membership dues per calendar year are: Active, $16.00; Student, $14.00; Sustaining, $25.00; Life memberships $250 (payable in four installments).

THE WILSON BULLETIN is sent to all members not in arrears for dues.

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Now two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution, thus making available to all Society members the more important new books on ornithology and related subjects. The fund will be administered by the Library Committee, which will be happy to receive suggestions on the choice of new books to be added to the Library. William A. Lunk, University Museums, University of Michigan, is Chairman of the Committee. The Library currently receives 195 periodicals as gifts and in exchange for *The Wilson Bulletin*. With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to: The Josselyn Van Tyne Memorial Library, University of Michigan Museum of Zoology, Ann Arbor, Michigan 48109. Contributions to the New Book Fund should be sent to the Treasurer (small sums in stamps are acceptable). A complete index of the Library's holdings was printed in the September 1952 issue of *The Wilson Bulletin* and newly acquired books are listed periodically. A list of currently received periodicals was published in the December 1978 issue.

THE WILSON BULLETIN
(ISSN 0043-5643)

The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September, and December. The subscription price, both in the United States and elsewhere, is $20.00 per year. Single copies, $4.00. Subscriptions, changes of address and claims for undelivered copies should be sent to the OSNA, Box 21160, Columbus, Ohio 43221. Most back issues of the *Bulletin* are available and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Joselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan 48109. Known office of publication: Department of Zoology, Ohio State University, 1827 Neil Avenue, Columbus, Ohio 43210.

Second class postage paid at Columbus, Ohio and at additional mailing office.

© Copyright 1982 by the Wilson Ornithological Society

Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

Socorro Mockingbird (*Mimodes graysoni*), Socorro Island, Mexico, April 1978.
Photograph by Joseph R. Jehl, Jr.

THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY

Published by the Wilson Ornithological Society

VOL. 94, NO. 1 MARCH 1982 PAGES 1–104

Wilson Bull., 94(1), 1982, pp. 1–19

THE STATUS OF THE AVIFAUNA OF THE REVILLAGIGEDO ISLANDS, MEXICO

JOSEPH R. JEHL, JR., AND KENNETH C. PARKES

Despite their relative proximity to Baja California and the Mexican mainland, the Revillagigedo Islands (frequently but erroneously written "Revilla Gigedo," Richards and Brattstrom 1959:328) have been visited only infrequently by scientists. The avifauna of these four islands (in descending size, Socorro, Clarión, San Benedicto and Roca Partida) has been reviewed most recently by Brattstrom and Howell (1956).

In April 1978, a Carnegie Museum of Natural History/Hubbs-Sea World Research Institute expedition visited Socorro and San Benedicto islands, which are located between 370 and 400 km (230–250 miles) south of the tip of Baja California. The trip was prompted by rumors of the development of an airstrip on Socorro. Our purpose was to determine the status of the endemic birdlife, and to obtain anatomical material and sound recordings, which had not been available previously, for taxonomic studies. A second expedition, in April 1981, was directed at clarifying the status of several species in light of our earlier findings.

In this paper we review the results of those expeditions and summarize the findings of several other trips to the islands. Mainly we present data that amplify the findings of Brattstrom and Howell (1956). Specimens collected in 1978 went to the Carnegie Museum of Natural History (CM); a few were exchanged to the Royal Ontario Museum (ROM), and one Townsend's Shearwater (*Puffinus auricularis*) specimen went to Hubbs-Sea World Research Institute (HSWRI). Weights for endemic land birds are listed. No specimens were obtained in 1981.

Descriptions and maps of the Revillagigedos, including place names used in this report, may be found in Richards and Brattstrom (1959; see also Fig. 1).

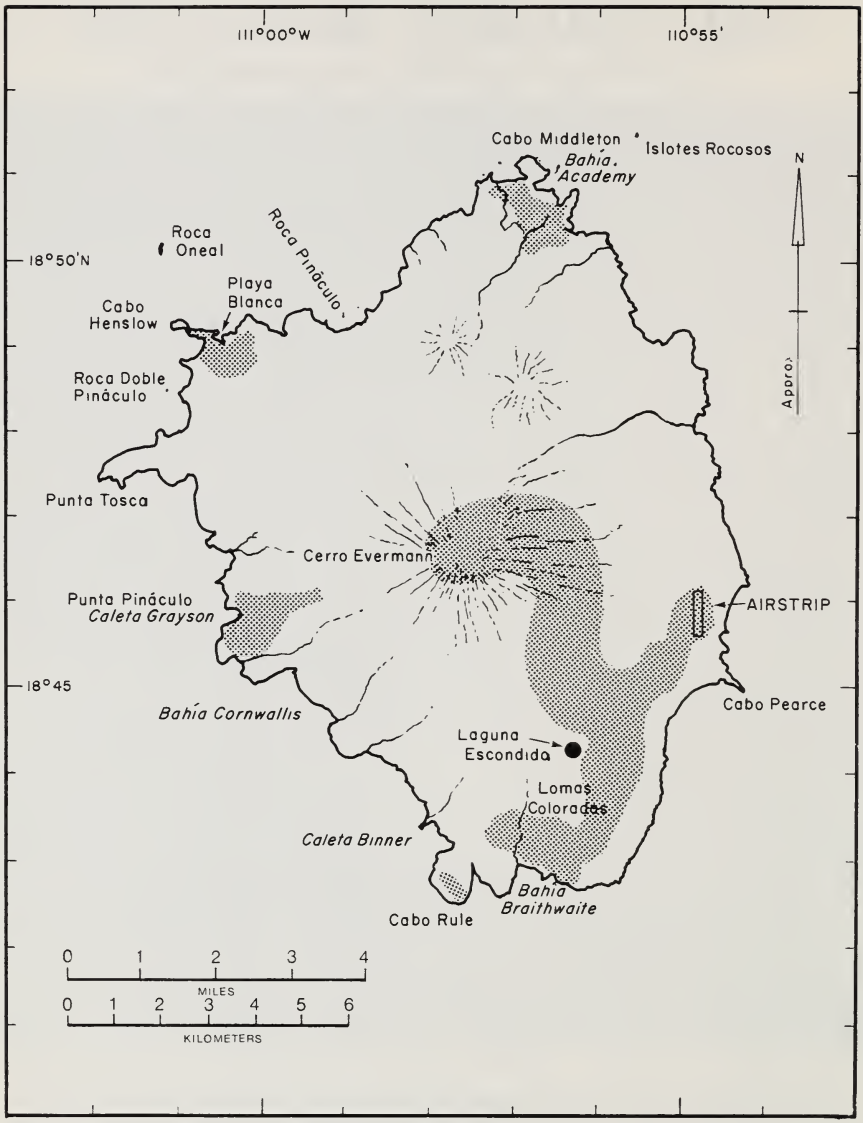


FIG. 1. Socorro Island (after Richards and Brattstrom 1959). Stippled areas were investigated by field parties in either 1978 or 1981.

ITINERARY AND FIELDWORK

We departed Puerto Vallarta, Mexico, on 8 April 1978, arriving at Socorro on 9 April. We spent 10 April in the vicinity of Caleta Grayson (Grayson's Cove); 11 April at Cabo Henslow

(Playa Blanca); 12–13 April near the airstrip and the east side of Cerro Evermann (the central peak of Socorro), and between the airstrip and the military garrison at Bahía Braithwaite; 14 April at Academy Bay; 15 April at Caleta Grayson and at sea 2–8 km off the east side of the island. On the afternoon of 15 April we departed for San Benedicto Island, arriving in the late afternoon. The 16th was spent ashore, and in the early evening we departed for Cabo San Lucas, Baja California, arriving on the morning of 18 April. The scientific party consisted of J. C. Barlow, B. H. Brattstrom, J. R. Jehl, Jr., R. V. Moran, K. C. Parkes and R. L. Pitman.

On 3 April 1981, Brattstrom, Jehl, Moran and Parkes departed Cabo San Lucas, arriving at Socorro early on 4 April. Jehl, Parkes and Moran spent 4–6 April ashore, mainly in the forested areas at 500–1040 m on the east and north sides of Cerro Evermann. Other observations were made in the dry wooded and open areas between Cerro Evermann and Bahía Braithwaite on 6 April. We also visited the small temporary lake described by Brattstrom and Howell (1956) and known to the inhabitants as Laguna Escondida. Brattstrom made additional observations in the vicinity of Bahía Braithwaite and the military garrison (4 April), Bahía Academy (5 April), and Caleta Grayson (6 April). On 7 April, Brattstrom, Moran and Parkes investigated the Cabo Henslow area, while Jehl made observations on seabirds at Roca Oneal and elsewhere on the east and north sides of the island. The evening of 7 April and the morning of 8 April were spent in a brief survey of San Benedicto. We returned to Cabo San Lucas on the 9th.

Other studies.—In April 1955, January 1956, August 1961 and November 1971, Brattstrom made additional notes on the avifauna as part of his intensive and long-term studies of the islands.

In November 1974, Jehl and Pitman, aboard the R/V Hero en route to South America, passed close by Socorro on the morning of 18 November. Mechanical problems forced the ship to return to Bahía Braithwaite, and between 21 and 25 November they made observations of all birds passing near the ship, which was anchored approximately 2 km off the coast; land-based studies were not feasible.

In the following annotated list, species not listed for the Revillagigedos by Brattstrom and Howell (1956) are indicated by an asterisk.*

ANNOTATED LIST OF SPECIES

*Pied-billed Grebe (*Podilymbus podiceps*).—Brattstrom found one dead on the beach at Cabo Henslow, Socorro, on 14 November 1971 (preserved California State Univ., Fullerton).

*Black-footed Albatross (*Diomedea nigripes*).—A specimen in CM was collected by A. W. Anthony at sea 24 km N of San Benedicto on 3 June 1897, but not listed by Anthony (1898) in his paper on the avifauna of the islands, unless this was the bird mentioned as having been "seen a short distance from Clarión."

*Pink-footed Shearwater (*Puffinus creatopus*).—One 45 km N of San Benedicto, 8 April 1981.

Wedge-tailed Shearwater (*P. pacificus*).—In November 1974, a few were seen daily at Bahía Braithwaite. On 15 April 1978, 30 fed along with 200 Townsend's Shearwaters 2–8 km W of Socorro. On 15 April 1978 and on 7 April 1981, 50 and 363 shearwaters, respectively, were counted off the

south coast of San Benedicto, as the birds began to stage prior to arrival at the nesting areas. A flock of ca. 150, mixed with other seabirds, was feeding over a school of tuna 30 km N of San Benedicto on 8 April 1981.

In 1978 Pitman estimated 1000 burrows near the top of Herrera Crater and Volcán Bárcena on San Benedicto; none was occupied. In 1981 Jehl saw a few hundred burrows on the rim of Herrera Crater; many had fresh footprints at the entrances but all checked were empty.

Anthony (1898) said that around San Benedicto and Socorro, the only places he saw this species, the sooty plumaged outnumbered the light-bellied by about two to one. He also stated that, in his series of 75 specimens, there was much variation in color of the underparts. This variation is confirmed by 52 Anthony specimens from San Benedicto now in CM. Although at least half would be characterized as "dark," there is such a spectrum that delimiting "dark," "intermediate" and "light" would be arbitrary. King (1974) reviewed the distribution of color phases in several Pacific Ocean colonies and, although giving the proportion of light birds at San Benedicto as 33% or less, based on data from the literature, he correctly inferred that the percentage was probably much less. At present the dark birds comprise virtually the entire population. In 1978 only four of over 300 birds were light-phased, and in 1981 only one of about 600. In 1981 we also saw and photographed a half dozen individuals of intermediate" appearance, with relatively dark backs, dusky bellies and smudgy underwings.

Townsend's Shearwater (*P. auricularis*).—Common 2–8 km off Socorro in 1974, 1978 and 1981. In November 1974, small flocks totalling a few hundred birds staged well off the south coast in early evening. We were unable to reach the nesting areas on Cerro Evermann in 1978, although we heard one bird calling over the island, near the airstrip, on 12 April. The shearwaters were very common over the island on 5–6 April 1981 and hundreds flew over our camps at 500–650 m altitude, beginning about one h after sunset. Evidently the major breeding sites are between 650–850 m. Despite checking many burrows in the soil and suitable crevices in rocky outcrops we found no nests so that we are unable to suggest the stage of the breeding cycle. We found the remains of four shearwaters that had been killed, almost certainly by feral cats (*Felis catus*). There are no other predators on the island except the diurnal Red-tailed Hawk (*Buteo jamaicensis*) (see also, Barn Owl [*Tyto alba*]). Although the number of kills was small, all carcasses were discovered within a few meters of the trail to the top of the island, which leads us to suspect that the carnage is more extensive.

*Galapagos Storm-Petrel (*Oceanodroma tethys*).—In November 1974 this storm-petrel was uncommon but regular in the general vicinity of Socorro.

TABLE 1
BOOBY POPULATIONS AT SAN BENEDICTO ISLAND

Species	No. nesting pairs[a]		No. individuals[b]	
	1978	1981	1978	1981
Sula dactylatra	1500–2000	1000	several 1000's	2000
Sula leucogaster	4	1+	23	20
Sula sula	60	?	877	400

[a] Based on counts in the breeding colonies.
[b] Estimated from numbers of birds returning to the colony at sunset.

Red-billed Tropicbird (*Phaethon aethereus*).—One or two were seen almost daily within 2–8 km of Socorro in 1974, 1978 and 1981. On 7 April 1981, Jehl saw two to four pairs courting over Roca Oneal, where they doubtless breed. Barlow found a nest on the lava delta on San Benedicto on 16 April 1978; it contained a nearly fledged chick. Pitman reported ten birds (but no evidence of nesting) near the top of that island on the same date.

Blue-footed Booby (*Sula nebouxii*).—Nelson (1978:447) stated: "At one time, though perhaps not now, San Benedicto and perhaps Clarión seem to have been the only islands in the world upon which four species of boobies nested (white [masked], brown, red-footed and blue-footed)." No documentation is offered for this statement with respect to Clarión; for San Benedicto Nelson (1978:517) presented a statement in quotation marks: "hundreds of pairs nesting on the slopes July 1939," but failed to specify the source. There is no obvious source for such a statement among the works listed in Nelson's bibliography. None of the early avifaunal reports mentioned the Blue-footed Booby in the Revillagigedos. We regard the reported breeding of this species on San Benedicto as dubious, at best. That it is an occasional visitor to San Benedicto rests on the evidence of Brattstrom (1963) and Brattstrom and Howell (1956), who reported three on 17 November 1953, and Parkes, who tentatively identified one over the lava delta on 8 April 1981.

Masked Booby (*S. dactylatra*).—In November 1974, April 1978 and April 1981, one to four were seen daily at Socorro. Yet, at San Benedicto, only 48 km away, the species is abundant. In both 1978 and 1981 we counted birds arriving at the island at dusk (Table 1). On the island Pitman estimated 1500–2000 nests in various stages, from single eggs to one with a one-third grown chick. The largest nesting concentrations were on the west side of Herrera Crater. No immatures were in the colony and we saw only one in the entire area. In 1981 Jehl counted a minimum of 937 nests

in Herrera Crater; at a few only paired adults were in attendance; most contained eggs and chicks to 2 weeks old. A few large downy chicks were present, but none in juvenal plumage. Only two immatures were seen near the island.

Red-footed Booby (*S. sula*).—One or two could be seen daily within 2–8 km of Socorro in 1974, 1978 and 1981. At San Benedicto, on 16 April 1978, the colony on the lava delta contained about 40 pairs; other smaller colonies were at Punta Oaxaca and Trinidad Rocks. At least a half-dozen pairs were nesting on the delta on 8 April 1981, but the colony could not be fully surveyed.

All of the birds at Socorro and the vast majority at sea near San Benedicto were in intermediate or dark phase, whereas, in 1978, approximately 80% of the nesting birds were light phased, 20% intermediate or dark. Several mixed pairs were present.

Although Brattstrom and Howell (1956) failed to comment on the point, the relative abundance of the boobies on San Benedicto has changed substantially since 1897. Anthony (1898) found *S. sula* "by far the most abundant species on the island." *S. dactylatra* was "common," and *S. leucogaster* "about as common as [*S. dactylatra*]." Anthony did not mention *S. nebouxii*. The breeding season for *S. sula* in 1897 was later than in 1978 or 1981. Anthony took fresh eggs on 1 May, and found that second sets had been deposited in the same nests on 17 May. "A few young were found on the latter date." In contrast, on 16 April 1978 and 8 April 1981, Parkes found young of all sizes in the Lava Delta colony, from small downy squabs to fully-feathered juveniles still at nests with their parents.

Brown Booby (*S. leucogaster*).—One or two were seen daily at Socorro in 1974, 1978 and 1981. At San Benedicto this was by far the rarest of the boobies; only five were seen returning to roost on the evening of 15 April 1978, and eight on 7 April 1981. In 1978 Pitman found four nests, one with one egg, one with a small chick and two with single chicks nearly ready to fledge. In 1981 Jehl saw one nest, which he was unable to reach.

Great Frigatebird (*Fregata minor*).—This species was never identified at Socorro nor at sea near the islands. It is fairly common at San Benedicto, however. In 1978 Pitman reported about 50, including some newly fledged young, roosting on the northwest side of the island. On the north side of Herrera Crater he found about 50 birds and five nests, two containing an egg each and three at which adults were incubating or brooding; a few fledglings were present. In 1981 we discovered a colony of about 50 pairs on a steep cliff on the northwestern side of the island; the area was not approachable by land and the contents of the nests were undeterminable. An adult and an immature female were collected on 16 April 1978; the adult showed little or no body molt and the largest ova were 2

mm in diameter; the immature was not molting. Brattstrom (pers. comm.) found frigatebirds (almost certainly *F. minor*) nesting on Roca Partida in 1971, but could not determine the species.

*Magnificent Frigatebird (*F. magnificens*).—Although all authors through Brattstrom and Howell (1956) have reported only *F. minor* from the Revillagigedos, all of 5–10 frigatebirds seen at Socorro in November 1974, April 1978 and April 1981 were clearly *magnificens*. Magnificent Frigatebirds were also seen at San Benedicto. In April 1978 both species were present, in seemingly equal numbers, near the lava delta. Two females of *magnificens* were collected; neither had ova greater than 2 mm in diameter, and one was in heavy molt. In 1981 several *magnificens* were present at that locality, but *minor* predominated.

F. magnificens and *F. minor* are known to be sympatric only in the Galápagos. As frigatebirds do not normally wander far from the immediate area of nesting colonies, the presence of an adult male Magnificent Frigatebird with enlarged testes (19 × 13 mm) collected at Bahía Academy, Socorro, on 14 April 1978, suggests that this species may nest in the extensive areas of wooded habitat there.

*Cattle Egret (*Bubulcus ibis*).—While anchored at Socorro on 21–25 November 1974, Pitman and Jehl watched flocks of 11, 19 and 35 arrive at the southern end of the island in the early morning. In 1981 at least six to eight were present at the military base on Socorro, and the base commander informed Jehl that he believed some remained year-round.

Snowy Egret (*Egretta thula*).—Considered "casual" on Clarión by Brattstrom and Howell (1956). Brattstrom reported four egrets, presumed to be Snowy, on Clarión on 9 November 1971, but did not consider the possibility of Cattle Egrets, which were invading Baja California in that period (Power and Rising 1975).

Yellow-crowned Night Heron (*Nyctanassa violacea gravirostris*).—This endemic race, resident on Socorro, is evidently very secretive. Only one was actually seen in 1978, a few hundred meters inland at Bahía Academy, and none was seen in 1981. However, we heard calls at night on the east side of the island, saw footprints at Playa Blanca and Bahía Academy, and found numerous middens of crab remains, some on the edge of high cliffs overlooking the sea, all ample proof of the continued presence of the heron.

*Duck (*Anas* sp.).—Brattstrom saw a duck, similar to a female Mallard (*A. platyrhynchos*), in a pond on Clarión on 8 November 1971. Except for a sight record of Blue-winged Teal (*A. discors*) on Clarión (Brattstrom and Howell 1956), this is the only record for an anatid in the Revillagigedos, unless one accepts literally the observations in the fall of 1793 of Captain James Colnett, who "made no attempt to visit the interior of Socorro, but

assumed the existence of a freshwater lake in the hinterland, because of the number of teal in flight" (McLellan 1925).

Red-tailed Hawk (*B. j. socorroensis*).—Found everywhere on Socorro. At least one pair was present at each area we visited including Caleta Grayson, Bahía Academy, the east side and crest of Cerro Evermann, Playa Blanca and Bahía Braithwaite. Brattstrom reported three at Cabo Middleton in 1971. We estimated the population at 15–25 pairs.

There are no native mammals on Socorro. Brattstrom and Howell (1956) conjectured the hawks may often feed on lizards, as "the lizards of Socorro are much warier than the related species on Clarión, where no hawks are resident." Land crabs are also an important component of their diet (Grayson 1872; Brattstrom, pers. comm.). McLellan (1926) described a pair feeding on a small lamb (carrion?). Villa (1960) described the capture of ground-doves (*Columbina*) by Red-tailed Hawks, and McLellan (1926) found the remains of *Zenaida graysoni* in the crop of a hawk specimen. Villa (1960) stated that in 1958 the military detachment protected all birdlife except the Red-tailed Hawks, as the latter preyed on birds, which they pursued even through the encampment. Those marines authorized to hunt sheep shot hawks when they had the opportunity. We doubt that the practice of shooting hawks continues and the hawk remains abundant.

All published descriptions of this race seem based on the type series of three birds in pale or "normal" plumage in the National Museum of Natural History. Consequently, comparisons (e.g., Friedmann 1950) have been made with the pale phase of *B. j. calurus*. Either the collection of these three specimens was a sampling accident or the color phase structure of the Socorro population has changed. We found *socorroensis* to be highly variable but predominantly melanic (65–75% of 20 birds observed), although none reached the blackish extreme of *calurus* illustrated by Taverner (1927:pl. III.). One rather dark adult female collected at Bahía Academy on 14 April 1978 is similar to a female *calurus* (CM 136425) from the Mackenzie Delta, N.W.T., Canada. We find that *socorroensis* cannot be separated from *calurus* on the basis of color and the validity of *socorroensis* must rest on its more robust legs and feet. The diameter of its tarsi and toes is obviously greater, but this is not revealed by standard linear measurements; comparative measurements should be made on osteological material, which is not available for the island form.

As all of the published measurements of *socorroensis* are derived from the type series, we present those of our adult female, and compare them with those of the single female (in parentheses; from Friedmann 1950) in the USNM: wing chord 385 (415); tail 215+ [very worn] (232); culmen from cere 27.7 (29.5); tarsus 93.5 (90); middle toe without claw 52.7 (50); weight 1260 g [little fat] (not available for other specimen).

Osprey (*Pandion haliaetus*).—Considered "accidental on San Benedicto and Socorro" (Brattstrom and Howell 1956), but probably a regular winter visitor, as it is in the Galápagos far to the southeast. Brattstrom reported two on Socorro in 1971. We saw one over Caleta Grayson on 10 April 1978, one at Cabo Henslow on 11 April, and one at San Benedicto on 16 April.

Peregrine Falcon (*Falco peregrinus*).—Listed by Brattstrom and Howell (1956) as "accidental on Socorro." Pitman saw one at San Benedicto on 16 April 1978, and Brattstrom reported one on San Benedicto on 8 April 1981.

*Black-bellied Plover (*Pluvialis squatarola*).—Three birds on a denuded plain near the airstrip on Socorro on 13 April 1978. This species may have been the "large Plover" seen by Anthony (1898) on Clarión in 1897, with a Golden Plover (*P. dominica*) alongside for size comparison.

Semipalmated Plover (*Charadrius semipalmatus*).—Listed by Brattstrom and Howell (1956) as "accidental on Socorro." Additional records include one collected at Bahía Academy, Socorro, (Brattstrom, pers. comm.) on 3 May 1955, and one on Socorro, 11 April 1978.

*Killdeer (*C. vociferus*).—Brattstrom reported two on Clarión on 8 November and one on 9 November 1971. Parkes heard one at the lake on Socorro on 6 April 1981.

Whimbrel (*Numenius phaeopus*).—Considered by Brattstrom and Howell (1956) to be casual on the three main islands, but probably regular in winter. There are additional records for Clarión (1971), Socorro (1955, 1971, 1981), and San Benedicto (1978).

*Long-billed Dowitcher (*Limnodromus scolopaceus*).—The remains of a very large individual of this species (presumably a female) were found at the mouth of a Burrowing Owl (*Athene cunicularia*) burrow on Clarión in November 1971.

Western Sandpiper (*Calidris mauri*).—One was seen at Laguna Escondida, Socorro, on 6 April 1981. There is one record from Clarión in March 1953 (Brattstrom and Howell 1956). Brattstrom also saw a "peep" (*C. mauri* or *C. minutilla*) on Clarión in 1971.

*Northern Phalarope (*Phalaropus lobatus*).—One was seen by Brattstrom at Clarión in 1971. A few small flocks were present between Socorro and San Benedicto in 1981.

*Pomarine Jaeger (*Stercorarius pomarinus*).—Two were noted at Bahía Braithwaite, Socorro, on 18 November 1974.

*Heermann's Gull (*Larus heermanni*).—A partial skeleton, found at Playa Blanca, Socorro, 11 April 1978, was identified by Parkes.

*California Gull (*L. californicus*).—A first-winter bird was collected at Socorro in November 1974 (specimen in San Diego Natural History Museum).

*Glaucous-winged Gull (*L. glaucescens*).—Jehl and Pitman collected a first-year bird at Bahía Braithwaite, Socorro, 21 November 1974 (specimen SDNHM).

*Laughing Gull (*L. atricilla*).—One immature observed at Socorro on 21 November 1974.

*Franklin's Gull (*L. pipixcan*).—Dr. Charles Hogue, Los Angeles County Museum, photographed an adult at Socorro on 7 June 1977 (identification confirmed by Jehl).

*Sabine's Gull (*Xema sabini*).—A partial skeleton from San Benedicto, 16 April 1978, was identified by Robert W. Storer.

Brown Noddy (*Anous stolidus*).—Anthony (1898) described the collecting of the type series of *A. s. ridgwayi* (now in CM) on 12 May 1897, from a large nesting colony (also containing many Sooty Terns [*Sterna fuscata*]) "on a rock a mile off the southwest point of the island [i.e., Socorro]." ("Southwest" was undoubtedly a *lapsus* for "northwest." Kaeding (1905), who accompanied Anthony, described the rock as "lying a few miles to the northward of Socorro Island.") This description fits Roca Oneal, where the species was said by Brattstrom and Howell (1956) to nest. On 7 April 1981, we saw 20 along the east side of Socorro and a few others between Socorro and San Benedicto.

*Mourning Dove (*Zenaida macroura*).—The occurrence of this species on Socorro was totally unexpected. It has invaded the island since 1958 (and perhaps 1971, the date of Brattstrom's most recent trip prior to the 1978 expedition), and by 1978 had established itself as an abundant breeder on the SE side, between the airstrip and Bahía Braithwaite. The party saw 100 or more near the airstrip on 12–13 April 1978, heard several calling in the early evening, saw courtship flights, and found one nest with two eggs, one nest containing two squabs, and several deserted nests. A large flock was seen on 12 April by Parkes and Brattstrom on the weedy hillside between Km 4 and Km 5 on the road from the airstrip to Bahía Braithwaite.

In 1981, the doves remained abundant in the lowlands on the southeast side of Socorro, and over 100 were seen in trees adjoining the small lake. We also recorded them sparingly well into the forested areas to 650 m.

These doves were very wary and difficult to approach. In all respects, including voice (recorded by J. C. Barlow in 1978) they seemed identical to *Z. m. marginella*. Two adults and two squabs taken in 1978 show no trace of introgression with the endemic Socorro Dove, nor do they resemble the distinctively proportioned endemic Clarión subspecies (*Z. m. clarionensis*). In 1981, we made careful observations of over 100 individuals, again failing to detect any obvious signs of hybridization with *socorroensis*. Brattstrom found a single Mourning Dove on San Benedicto on 8 April 1981, the only record for that island.

Socorro Dove (*Z. graysoni*).—This dove was once common on Socorro, and existed there as late as 1958 (Villa 1960). We failed to find it, despite intensive efforts in 1981, and presume that it is extinct in the wild. The history of this species will be discussed separately (Jehl and Parkes, unpubl.).

Common Ground-Dove (*Columbina passerina socorroensis*).—Common on Socorro in dry woodlands and open areas on the S and SE slope, in the garrison, along the road to the airstrip, at Playa Blanca, Cabo Rule, and Caleta Grayson. At the latter locality a flock of 40 were present at a small seep on the hillside on 15 April 1978. The species seemed rare and more local in 1978, perhaps because of the very dry conditions in that year. (Weight: 4 ♂♂—32.5–39 [36.2] g; 2 ♀♀—32, 32.5 g.)

Green Parakeet (*Aratinga holochlora brevipes*).—This species was encountered in small flocks (3–10 birds, once 30) in heavily wooded areas above 500 m around Cerro Evermann. Though not particularly common, their raucous calls make them very conspicuous. (Weight: 3 ♂♂—150, 150, 155 g.)

Common Barn-Owl (*Tyto alba*).—Villa (1960) is the only author to have suggested the presence on Socorro of any owl other than the endemic Elf Owl. He stated that he found in a fig tree at Bahía Braithwaite "huellas inequívocas" of owls of this species, and that members of the naval detachment reported finding a nest with two young a few days earlier. Furthermore, on 18 January, while camped east of Laguna Escondida, he heard what he took to be "el monótono canto de varias de estas lechuzas." Although this owl is a notorious colonizer of islands, its presence on Socorro must be considered unproven.

Elf Owl (*Micrathene whitneyi graysoni*).—Villa (1960) did not encounter this species during his 1958 visit to Socorro, and mentioned no records subsequent to the specimens collected by Slevin in 1925 (McLellan 1926). However, he believed that it was still "más bien común" on the island, judging from information obtained from military personnel. To our knowledge, the most recent record is a specimen taken 27 March 1932 (Calif. Acad. Sci.). In 1978 Barlow, Pitman and Jehl listened for owls in the dry woodlands near the airstrip. And on two nights in 1981, using a tape recording, Jehl and Parkes tried unsuccessfully to elicit responses, in wooded areas at 500 m and 650 m. However, we were not ashore at night in the habitat in which McLellan described Elf Owls as "less rare than they were formerly supposed to be," i.e., "dense growth on the lower levels of the island"; Slevin's specimens were taken "in a tree at the bottom of an arroyo near Braithwaite Bay." Both adequate nesting cavities and grasshoppers, small crabs (Grayson 1872) and other suitable food for this owl are abundant.

Belted Kingfisher (*Ceryle alcyon*).—Considered accidental on Socorro and Clarión by Brattstrom and Howell (1956) but probably regular in winter. We saw several on Socorro in 1978 and Brattstrom reported three in various localities in 1971.

*Rough-winged Swallow (*Stelgidopteryx ruficollis*).—Two were seen at Bahía Academy, Socorro, 14 April 1978.

Common Raven (*Corvus corax clarionensis*).—Brattstrom and Howell (1956) considered the raven as a "regular visitor" on San Benedicto, but which bred only on Clarión. We saw no ravens on San Benedicto on either of our visits, nor did Brattstrom (1956) in 1953. There is no doubt, however, that the species formerly occurred there. Townsend (1890) called it "abundant," Anthony (1898) characterized it as "rather common" and Hanna (1926) considered it "not very abundant," but saw six. There are no records from Socorro, the most frequently studied island, only 43 km from San Benedicto. Thus, we doubt that ravens at San Benedicto were merely visitors from Clarión, 362 km away. More likely, they were residents which became extirpated prior to, or by, the eruption of Volcán Bárcena in 1952.

Brattstrom estimated the raven population on Clarión at 75–100 birds in 1955 and at 256 in 1971. The 1953 population was estimated by Brattstrom and Howell (1956) at 400–450 individuals.

Socorro Wren (*Thryomanes sissonii*).—This species, second in abundance to the Tropical Parula, occurred at every locality we visited on Socorro up to the crest of Cerro Evermann (1040 m). At Caleta Grayson it was outnumbered about 10:1 by the warbler and was most common in the woods near the shore; it also occurred in the brushy hillsides to the edge of the beach. This wren occurs in low strata and was almost always seen on or near the ground, seldom higher than 2 m in trees. Several families of wrens with recently fledged young were seen on 5–6 April 1981.

As noted by Brattstrom and Howell (1956) the generic relationships of the wrens on Socorro (*T. sissonii*) and on Clarión (*Troglodytes tanneri*) are uncertain. Preliminary data (Barlow, pers. comm.) support the transfer of the Socorro Wren to *Troglodytes*. (Weight: 6 ♂♂—8.5–11.0 (9.2) g; 3 ♀♀—9.3, 9.7, 10.0 g; 5 sex?, 8.5–10.0 (9.2) g.)

Rock Wren (*Salpinctes obsoletus exsul*).—Like other observers since the eruption of Volcán Bárcena in 1952, we failed to find this endemic wren on San Benedicto, and agree with Brattstrom and Howell (1956) that it is extinct.

Northern Mockingbird (*Mimus polyglottos*).—This species is another recent invader of Socorro. Brattstrom reported one at Caleta Grayson on 10 April 1978, and Parkes and Brattstrom saw two, about 300 m apart, in open country near Km 5 on the road to the airstrip on 12 April 1978. By April 1981, the species was abundant on the SE side of the island, up to

400 m elevation, in open and scrubby areas. On 6 April, we saw at least 30 individuals and found a nest with a large chick. The species is now restricted to this area of the island and there does not appear to be suitable habitat for it elsewhere. There is a previous sight record for Clarión (Brattstrom and Howell 1956).

Socorro Mockingbird ("Thrasher") (*Mimodes graysoni*).—This endemic mimid was considered by McLellan (1926) "the most abundant and most widely distributed species on Socorro. They were particularly numerous about the spring at Caleta Grayson, and in the heavily wooded cañons. Eight males (one immature) and two females were collected on May 3." Brattstrom (*in* Brattstrom and Howell 1956) found *Mimodes* "common at lower elevations" in March 1953, but noted no singing. In November 1953, they "appeared to be rare at lower elevations on the south side of Socorro but common in forested areas at higher elevations and in canyons on the north side of the island. Some aggressive behavior and much singing were noted at this season." Villa (1960) described the species as abundant in the higher wooded areas of the island in January 1958, and emphasized its extreme tameness; two that entered his camp fed on bread crumbs from his hand and one of these even perched on his shoulder and sang. In 1955 and 1971, Brattstrom (in litt.) found *Mimodes* as high as 700 m on the south side of Cerro Evermann.

In 1978, we saw *Mimodes* only at Playa Blanca (4 or 5), Caleta Grayson (1), Academy Bay (1, singing), and near the airstrip, where our party was able to find only two in two days of fieldwork. In 1981 we spent little or no time in areas where we had found this species previously. At Playa Blanca, Parkes, using a tape playback, elicited a distant vocal response, and later lured into the open what may have been the same (or a second) individual, which approached within less than 2 m but sang only weakly in response to the tape. Brattstrom did not see or hear *Mimodes* at Caleta Grayson or Bahía Academy.

Although *M. graysoni* was widespread in the recent past, it seems now to be almost entirely restricted to the vicinity of large fig groves near the coast. Such habitat is now very rare. Our visits to Socorro were not made at the optimum season for hearing songs, judging from the observations of Villa and Brattstrom, but the former conspicuousness and tameness of this species strongly suggest to us that it is indeed absent or exceedingly rare in most of its previous range. We suspect that the prospects for its survival are dubious.

This species is universally called "Socorro Thrasher" in the literature. While it is true that Lawrence (1871), following a manuscript of Baird, named it in the genus *Harporhynchus* (=*Toxostoma*), it bears little resemblance in the field to a thrasher. The birds appeared to us (and to Grayson

[1872], its discoverer) like rather plainly plumaged mockingbirds, somewhat more heavy-set than *M. polyglottos*. They run for long distances, but sometimes hop for short forays. Both on the ground and on branches or shrub tops they cock their tails in typical mockingbird fashion, but not in as sharp an angle. We saw them foraging along the beach at the edge of the vegetation, where they were relatively tame, and also in low shrubs and trees farther inland, near the airstrip, where they were shy. Of the three current Mexican field guides, only the illustration in Peterson and Chalif (1973:pl. 34) approaches accuracy; all three portray the iris as yellow, whereas in our specimens it was actually brownish red. (Weight: 2 ♂♂—71, 73 g; imm. sex?—58 g.)

*Tennessee Warbler (*Vermivora peregrina*).—One was seen at Bahía Braithwaite, Socorro, on 12 April 1978.

Tropical Parula (*Parula pitiayumi graysoni*).—Brattstrom and Howell (1956) stated: "These little warblers were fairly common at lower elevations on Socorro, but they seemed scarcer than the other endemic land birds although equally tame and easy to approach . . . No singing or territorial behavior was noted in either March or November." In April 1978 and 1981 the endemic "Socorro Warbler" was by far the most common land bird on Socorro, occurring from the beaches to within 50 m of the peak of Cerro Evermann. They were most abundant in wooded areas such as the fig groves at Caleta Grayson and the forested uplands at 500–800 m, but were also fairly common on the dry, brush-covered hillsides, where their actions were reminiscent of those of Orange-crowned Warblers (*Vermivora celata*) in the western U.S. In wooded areas they fed nearly everywhere on the branches, from less than 1 m above the ground (occasionally even descending briefly to the ground) to the treetops, even hanging from the tips of leaves like tits (*Parus* spp.). Although generally gleaners, they would make short aerial forays after flying insects.

Although songs were commonly heard in 1981 (less frequently in 1978, at approximately the same time of year), there was little or no evidence of territorial behavior. In several areas of food abundance, gatherings of as many as 30–50 were seen; "squeaking" inevitably attracted groups of six to ten or more. There are several distinctive songs, plus a number of variations on these. The commonest is highly reminiscent of the simple song of the American Redstart (*Setophaga ruticilla*); another is closely similar to that of the Northern Parula (*Parula americana*); a third is a *Dendroica*-like song terminating in emphatic syllables, rather like that of the Chestnut-sided Warbler (*D. pensylvanica*). In 1981, at our camps at 500 and 650 m, we found that the major song period was in the predawn hours, commencing as early as 03:00 and lessening considerably by 06:00. Sporadic singing could be heard throughout the day, and a second peak

occurred in the evening about 15–30 min prior to dark. (Weight: 2 ♂♂—6.0, 6.5 g; 4 ♀♀—6.0–6.5 [6.3] g; 5 sex? [See *Thryomanes sissonii*] 5.8–6.5 [6.1] g.)

*Yellow Warbler (*Dendroica petechia*).—One seen by Parkes at Bahía Braithwaite, Socorro, on 10 April, was clearly an immature male of one of the "Mangrove Warbler" subspecies, either *castaneiceps* of Baja California or *rhizophorae* of the Pacific mainland of Mexico, as evidenced by the extensively gray plumage with touches of yellow. Another, seen by Jehl in the same area on 12 April, belonged to one of the northern races (*amnicola* or *rubiginosa*).

Yellow-rumped Warbler (*D. coronata*).—Brattstrom reported a "Myrtle" Warbler on San Benedicto, 8 April 1981. There are no previous records for this eastern form on the islands. However, Villa (1960) reported seeing many "Audubon's" Warblers on Socorro in January 1958, and collected one.

*Townsend's Warbler (*D. townsendi*).—A male was collected on Cerro Evermann, 13 April 1978.

*Black-throated Green Warbler (*D. virens*).—Two females collected with the male Townsend's Warbler on 13 April were loosely associated with a flock of Tropical Parulas (Barlow and Pitman, pers. comm.).

Bay-breasted Warbler (*D. castanea*).—In addition to the San Benedicto specimen collected in November 1953 (Brattstrom and Howell 1956), Brattstrom photographed an immature male of this eastern vagrant on the same island on 15–16 November 1971 (photograph identification confirmed by T. R. Howell and J. R. Jehl, Jr.).

*American Redstart (*Setophaga ruticilla*).—One (female?) was seen on San Benedicto on 15 November 1971.

Rufous-sided Towhee (*Pipilo erythrophthalmus socorroensis*).—Brattstrom and Howell (1956) reported that the endemic towhee was "common on Socorro in the cactus and bush of the lower elevations but [they] were rare among the trees." We found them at most localities, at least to 650 m, but they were in general uncommon and scattered. Singing was infrequent. They may be more numerous than we recognized, but we doubt that their current abundance approaches that of 1953, or of 1958 when Villa (1960) considered them abundant and conspicuous throughout the island. These birds feed mainly on the ground, but also occasionally forage as much as 3–4 m above the ground near trunks and main branches of large trees. They seldom ventured into open scrub, a common habitat of this species elsewhere, but preferred wooded clumps. They were much shyer than mainland races, which respond, often dramatically, to "squeaking," which was not true of *socorroensis*. This shyness was in striking contrast to the experience of Anthony (1898), who found towhees to be

"uniformly confiding and often half a dozen would congregate within a few feet of a person, silently inspecting him with an air of trustful curiosity quite foreign to other species of the genus with which I am familiar." (Weight: 3 ♂♂—29, 30, 30 g; 4 ♀♀—29.5–35 (31.6) g.)

DISCUSSION

The 1978 visit to Socorro occurred during a very dry season (F. Urtaza, pers. comm.); few birds were breeding or singing. In 1981 the vegetation was much lusher and the temporary lake covered about 0.6 hectare, down from a winter maximum of about 1 hectare.

The breeding season for landbirds on Socorro may extend from November through May (Parkes, unpubl.), perhaps being affected by annual variation in rainfall. We suspect that the main breeding period typically occurs late in the year, for during our April visits we saw very few juveniles of any species. Although endemic landbirds may have been less conspicuous during our trips than at other seasons, we have no doubt that the low numbers of Rufous-sided Towhee and Socorro Mockingbird, and especially our failure to find the Socorro Dove, indicate a marked decline in their populations.

Reasons for the changes are not easy to discern. Large numbers of sheep roam over Socorro, having been introduced in 1869 by sailors. The sheep have severely modified the vegetation below about 600 m, particularly on the south and east sides of the island, and many areas are overgrazed and denuded of native plants. The activities of the sheep, alone, cannot have been sufficient to account for the changes, because the decline in some bird populations seems to have occurred since 1958.

A more significant influence may be the presence of a military garrison at Bahía Braithwaite. The garrison was established in 1957 and by 1981 had grown to approximately 125 persons, including military personnel, civilians and a few dependents. The presence of a human settlement invariably means the introduction of domestic animals. In 1971, Brattstrom was informed that feral cats could be found over most of the island; also present were 10 horses, 20 burros, some chickens and a few domestic pigeons. In 1978, the base commander informed us that he was aware of the problems caused by cats and that they were being shot on sight. Even so, we dispatched a litter of kittens near the airstrip and heard adults calling at night. In 1981, we saw no cats, but the shearwater remains on Cerro Evermann give evidence of their continued depredations, even in remote sectors.

It is a matter of conjecture whether the towhee, mockingbird and Socorro Dove were depleted by predators, but it seems likely since the major declines have occurred since the establishment of a permanent human

settlement. Further, the species most seriously affected are ground foragers, and all were described as having been exceptionally tame. Given the dismal record of cats on other islands (e.g., Guadalupe), it would be astounding if their impact on Socorro were negligible. The status of the mockingbird seems especially precarious. The wren and warbler, having more arboreal habits and occurring in abundance, are less likely to be affected. Townsend's Shearwater remains abundant, perhaps granted some respite by virtue of its nesting sites at high elevations, but evidence of predation is undeniable.

We can hardly be optimistic about the future of the endemic avifauna so long as feral animals continue to exist on Socorro, and we urge steps to eliminate or reduce their numbers before further irreversible changes occur. The completion of the airstrip in 1979 does not seem to have imposed any additional stress on the avifauna.

SUMMARY

This paper summarizes the status of birds on islas Socorro and San Benedicto based largely upon visits in April 1978 and April 1981, and presents additional data on Isla Clarión. Isla Socorro is in a state of change, seemingly as a result of increased human activities since 1958 and the consequent introduction of domestic animals. Nine endemic avian taxa have been described for Socorro. In the past two decades, several of these have shown sharp declines which seem largely attributable to predation by domestic cats. *Pipilo erythrophthalmus socorroensis* seems far less common than in the recent past. *Mimodes graysoni*, once described as the most common landbird on Socorro, is extremely rare and local and its condition seems precarious. *Zenaida graysoni* is apparently extinct. *Thryomanes sissonii*, *Aratinga holochlora brevipes*, *Columbina passerina socorroensis* and *Parula pitiayumi graysoni* remain common; indeed the warbler may have increased. We are unable to present any new data for *Nyctanassa violacea gravirostris* or *Micrathene whitneyi graysoni*. Two species have invaded Socorro. *Zenaida macroura* became well established between 1971 and 1978 and *Mimus polyglottos* between 1978 and 1981. Resident landbirds are absent from San Benedicto but seabird numbers have increased since the eruption of Volcán Bárcena in 1952. Notes on 25 species recorded for the first time are included.

ACKNOWLEDGMENTS

Most of the cost of the 1978 expedition was covered by grants from the M. Graham Netting Research Fund and the Edward O'Neil Field Fund of Carnegie Museum of Natural History. Additional funding was provided by Hubbs-Sea World Research Institute. The 1981 expedition was sponsored by Tom and Dorothy Hawthorne of San Diego, California, with additional support from the M. Graham Netting Research Fund. Jehl's fieldwork in 1974 was supported by a grant from the Office of Polar Programs, National Science Foundation.

Permission to conduct these studies in Mexican waters was granted by Sr. Walter Ocampo, Dirección General de Regiones Pesqueras, Departamento de Pesca, Sr. Ignacio Ibarrola Bejar, Dirección General de la Fauna Silvestre, and Ing. Juan Jose A. Reyes Rodriguez, Secretaría de Agricultura y Recursos Hidraúlicos. We also thank Dr. Jorge Carranza Fraser for his interest and assistance in our studies.

We are grateful to R. Vile and R. French aboard the Sea World (1978), and to K. Hallinan, M. Gibbs and J. Morales aboard the Tomcat (1981) for their assistance in our field studies.

Capt. F. Urtaza of the Mexican Navy provided support and hospitality during our visits to Socorro, and H. Herrera G. provided exceptional service as a guide in 1981.

We are especially indebted to Milton C. Shedd for his continued interest in and support of our work, and for the pleasure of his company in the field.

J. C. Barlow provided us with his field notes from the 1978 expedition, as well as a tape of *Mimodes* vocalizations. J. W. Hardy provided the tape of *Micrathene*. Suzanne I. Bond prepared the 1978 specimens brought frozen to San Diego. R. W. Storer and S. L. Olson assisted in identifying skeletal remains.

Finally, we owe a special debt to B. H. Brattstrom for sharing with us his exceptional knowledge of the Islas Revillagigedos, and for providing the baseline studies on which this report is based.

LITERATURE CITED

Anthony, A. W. 1898. Avifauna of the Revillagigedo Islands. Auk 15:311–318.

Brattstrom, B. H. 1963. Bárcena Volcano, 1952: its effect on the fauna and flora of San Benedicto Island, Mexico. Pp. 499–524 *in* Proc. 10th Pac. Sci. Congr.

——— and T. R. Howell. 1956. The birds of the Revilla Gigedo Islands, Mexico. Condor 58:107–120.

Friedmann, H. 1950. The birds of North and Middle America. Vol. 11. Pt. II. U.S. Natl. Mus. Bull. 50.

Grayson, A. J. 1872. List of Socorro birds collected by A. J. Grayson, May, 1867. Proc. Boston Soc. Nat. Hist. 14:290–302. [N.B.—This paper is usually cited as "Lawrence, 1871," but it was merely *edited* by Lawrence, the wording being entirely Grayson's, and it was actually published in 1872].

Hanna, G. D. 1926. Expedition to the Revillagigedo Islands, Mexico, in 1925. General Report Proc. Calif. Acad. Sci., 4th ser., 15:1–113.

Kaeding, H. B. 1905. Birds from the west coast of Lower California and adjacent islands. Condor 7:105–111, 134–138.

King, W. B. 1974. Wedge-tailed Shearwater (*Puffinus pacificus*). Pp. 53–95 *in* Pelagic studies of seabirds in the central and eastern Pacific Ocean (W. B. King, ed.). Smithson. Contrib. Zool. 158.

Lawrence, G. N. 1871. Descriptions of new species of birds from Mexico, Central America, and South America, with a note on Rallus longirostris. Ann. Lyceum Nat. Hist. 10:1–21.

McLellan, M. E. 1925. Expedition of the California Academy of Sciences to the Revillagigedo Islands. Science 62:171–173.

———. 1926. Expedition to the Revillagigedo Islands, Mexico, in 1925, VI. The birds and mammals. Proc. Calif. Acad. Sci., 4th ser., 15:297–322.

Nelson, J. B. 1978. The Sulidae. Oxford Univ. Press, Oxford, England.

Peterson, R. T. and E. L. Chalif. 1973. A field guide to Mexican birds. Houghton Mifflin, Boston, Massachusetts.

Power, D. M. and J. D. Rising. 1975. The Cattle Egret in central Baja California, Mexico. Condor 77:353.

Richards, A. F. and B. H. Brattstrom. 1959. Bibliography, cartography, discovery, and exploration of the Islas Revillagigedo. Proc. Calif. Acad. Sci., 4th ser., 29:315–360.

Taverner, P. A. 1927. A study of Buteo borealis, the Red-tailed Hawk, and its varieties in Canada. Bull. Victoria Mem. Mus. 48:1–21.

Townsend, C. H. 1890. Birds from the coasts of western North America and adjacent islands, collected in 1888–89, with descriptions of new species. Proc. U.S. Natl. Mus. 13:131–142.

VILLA, R. B. 1960. Vertebrados terrestres. La Isla Socorro, Monogr. Inst. Geofisica, Univ. Nac. Autónoma de México 2:203–216.

HUBBS-SEA WORLD RESEARCH INSTITUTE, 1700 SOUTH SHORES ROAD, SAN DIEGO, CALIFORNIA 92109 AND CARNEGIE MUSEUM OF NATURAL HISTORY, 4400 FORBES AVENUE, PITTSBURGH, PENNSYLVANIA 15213. ACCEPTED 12 NOV. 1981.

COLORPLATE

The colorplate Frontispiece of Socorro Mockingbird ("Thrasher") (*Mimodes graysoni*) has been made possible by an endowment established by George Miksch Sutton. Photograph by Joseph R. Jehl, Jr.

INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE

The following opinion has been published by ICZN in Bulletin of Zoological Nomenclature, Vol. 38, Pt. 4, 8 Dec. 1981: Opinion No. 1189 (p. 243) "Circinae in Aves and Mollusca: removal of the homonymy." ICZN cannot supply separates of decisions.

Wilson Bull., 94(1), 1982, pp. 20–30

AVIAN POPULATION FLUCTUATIONS DURING DROUGHT CONDITIONS IN PUERTO RICO

JOHN FAABORG

Few long-term studies describe population dynamics of tropical avian communities during normal or abnormal periods. Karr et al. (1982) reported comparable measurements of bird density and community structure in Panamanian forest over a period of nearly a decade and Willis (1974) has long-term data for selected species on Barro Colorado Island, Panama. Although Diamond (1971) and Terborgh and Faaborg (1973) reported supposed cases of turnover (change in species composition over time without change in the equilibrium species number (see Diamond and May 1977) in island communities (cases which have been questioned [Lynch and Johnson 1974]), no one has examined the role of actual population fluctuations in the turnover process.

Here I report on the population dynamics of a West Indian bird community over a 5-year period that included severe drought conditions. The effects of these conditions on total populations, populations of foraging guilds, and winter resident populations are shown. Possible reasons for differences among species are discussed, along with the way that such "ecological crunches" (Wiens 1977) may have led to patterns found in the Guanica Forest bird community.

STUDY AREA AND METHODS

This study was done in seasonally dry scrub in the Guanica Forest of southwestern Puerto Rico (for detailed habitat description see Terborgh and Faaborg 1973). The vegetation is situated on a limestone platform and is generally short and sclerophyllous, with many arboreal cacti.

Population size was determined by mist netting, as described earlier (Terborgh and Faaborg 1973). Net lines were operated from dawn to dusk, usually for 3 days. This allowed us to construct regressions of the capture rate of birds over time and to predict a total capture. On a couple of occasions only 2 days of netting were done; thus 2-day totals are used. Addition of the third day only accentuates the difference between good and bad periods, as the third day of netting during drought periods often yielded fewer than 10 birds. In all cases, the number of unbanded birds netted declined throughout the sample period, suggesting a resident population; during the drought period drastic drops in capture rates often occurred after the first day.

One line of 16 nets was operated in January of 1972. In 1973 a second line was erected and both lines were operated subsequently in January or early February of each year. The area was visited and netted in June of 1973, but due to possible seasonal differences in territorial behavior, these data are not presented here. All birds captured were banded, measured and released (for longevity records see Faaborg and Winters 1979, 1980), and age and sex were recorded when possible.

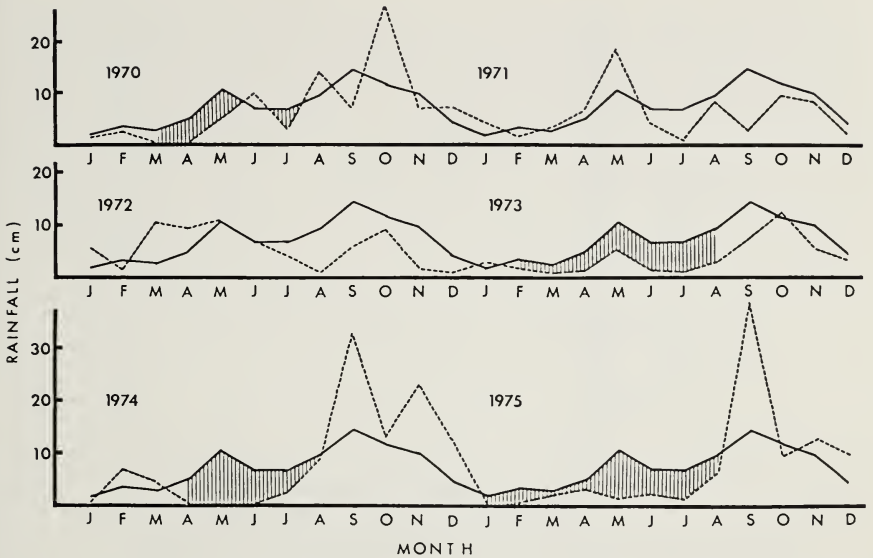


FIG. 1. Rainfall amounts for Ensenada for the period 1970–1975 (dashed line) with the normal amount (solid line). Shaded area designates a net deficit of rainfall during the first six months of a year. Data are from Calvesbert (1970 and supplements).

Rainfall data are from the U.S. Weather Bureau station at Ensenada, a coastal community 4 miles west of the study area. Average rainfall for this area is characterized by a small peak during May and a much larger peak in September and October. A dry season usually occurs from December to April.

The winter bird community can be separated into a permanent resident and winter resident component. The majority of breeding by permanent resident species, plus a few summer residents, occurs from late April to June (Wetmore 1916, Bond 1943), although a few species (mostly frugivores and nectarivores) breed at other times. Most non-breeding species arrive in September and stay until April, a period that encompasses both the wettest and driest parts of the year. Virtually all of these winter residents are gleaning insectivores (Faaborg and Terborgh 1980). Permanent residents were divided into the simple foraging guilds of frugivore (including both fruits and seeds), flycatching insectivore, gleaning insectivore, and nectarivore based upon known diets and foraging habits (Wetmore 1916).

RESULTS

Drought conditions.—Monthly rainfall totals for 1970–1975 are shown graphically in Fig. 1 along with the normal monthly amounts. One year was near normal, three were below normal (one nearly 40 cm below), and two were above normal in annual rainfall. However, annual rainfall may not be the best way to understand the effect of climate on bird populations in a habitat such as this, one in which potential evapotranspiration nearly always exceeds rainfall. Rather, the length and severity of the dry season

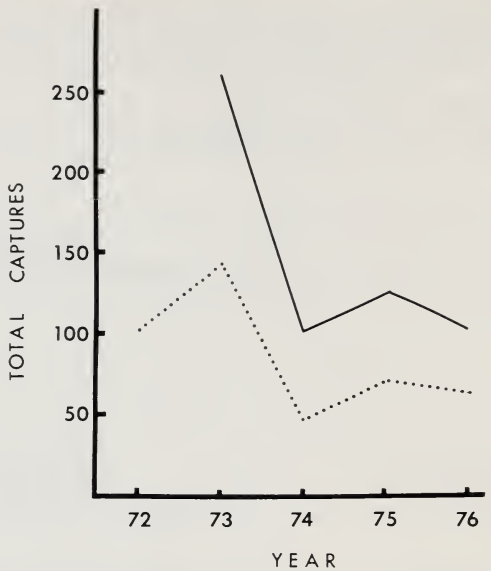


FIG. 2. Population fluctuations of the total resident bird population for 16-net, two-day samples over five years (dotted line) and 32-net, two-day samples over four years (solid line).

and the occurrence of rains before and during the breeding season may be critical. The yearly totals are greatly affected by heavy autumn rains occurring after the breeding season and often associated with tropical storms.

As shown in Fig. 1, the period 1970–1972 was characterized by normal or above normal precipitation before and during the breeding season. The fall rains did not occur to any extent in 1972 and the dry season started over a month early. Below normal rainfall characterizes 10 months of 1973, with the first 6 months running less than one-half the normal amount (13.54 cm vs 29.90 cm). While the fall of 1973 was about normal, the first 6 months of 1974 were drier than 1973 (12.17 cm). The drought was broken by heavy rains in the fall of 1974 and again in the fall of 1975, although the first 6 months of 1975 were very dry (7.85 cm). Thus, after three relatively normal years, the breeding seasons of 1973 through 1975 were characterized by drought conditions, while the dry seasons of 1972–73 and 1973–74 were relatively severe.

Population fluctuations of resident birds.—Fig. 2 shows population fluctuations for the total sampled community for the single netline (1972–1976) and the combined netlines (1973–1976). (Capture data by species and guild are listed in the Appendix.) Total populations were high in 1972 and

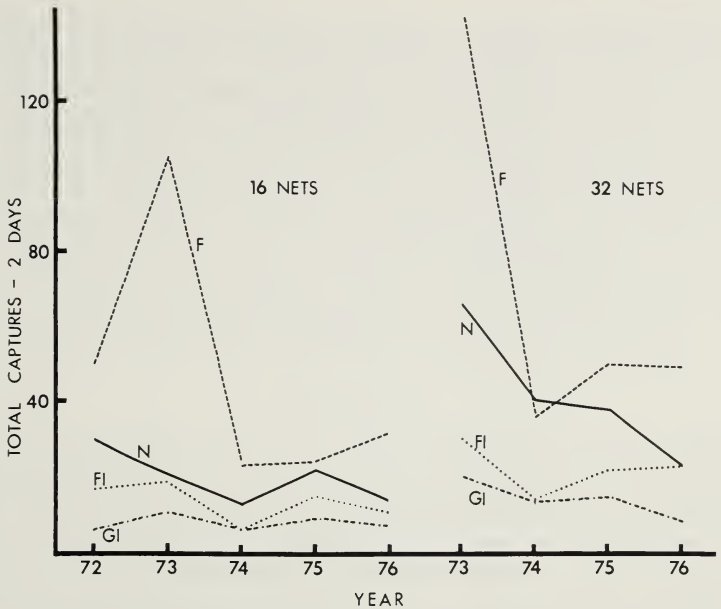


FIG. 3. Population fluctuations by guild for the 16-net, two-day sample over five years (left side) and the 32-net, two-day sample over four years (right side). F is frugivore, N is nectarivore, FI is flycatching insectivore and GI is gleaning insectivore.

peaked in 1973. Observations during June of 1973 revealed no active breeding; by January of 1974 the total population had declined sharply to less than 40% of its peak. The 1974 sample showed only about 6% juvenile birds and a high recapture rate of previously banded birds. A slight population increase occurred in 1975 followed by a slight reduction in 1976.

Fig. 3 shows the population fluctuations of resident birds by guild. The largest decrease occurred with frugivores, which also showed the greatest increases in 1973 and 1975. Resident gleaning insectivores declined relatively slowly from the 1973 peak, while flycatching insectivores declined sharply in 1974 but recovered somewhat in 1975 and 1976. Captures of nectarivores (the Bananaquit and two hummingbirds) decreased in 1973, probably as a result of a lack of flowers resulting from the early dry season. This decline continued throughout the remainder of the study. Hummingbirds had virtually disappeared from the Guanica Forest by 1975 and Bananaquits behaved largely as a gleaning insectivore during the drought.

The greatest single-species declines were also shown by frugivores. The Common Ground Dove fluctuated from 54 to 2 individuals during the crash while Puerto Rican Bullfinches dropped from 49 to 16 and the Black-faced

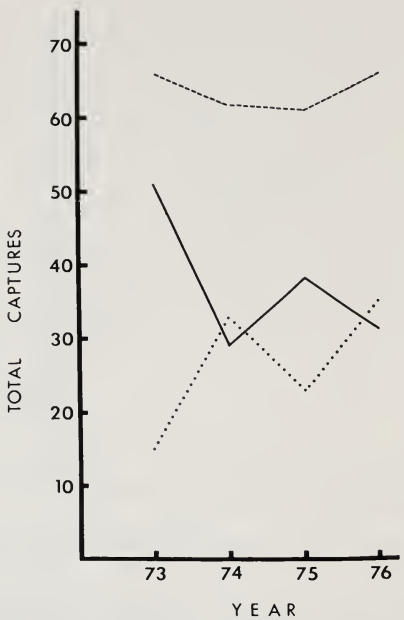


FIG. 4. Population fluctuations of winter residents (dotted line) and permanent resident insectivores (gleaners and flycatchers, solid line) with the total density of wintering insectivores (dashed line).

Grassquit from 29 to 6. Two of the largest frugivores (the Pearly-eyed Thrasher and Red-legged Thrush) actually increased in numbers during the severest part of the drought.

The flycatching Puerto Rican Tody declined steadily and the Stolid Flycatcher decreased by half in 1974 but recovered in 1975 and 1976. Among gleaning insectivores, only the Puerto Rican Vireo showed a substantial drop (7 to 2), while others declined slowly. The Bananaquit and Antillean Mango demonstrated similar decreases in 1974, but the hummingbird continued to decline in subsequent years, whereas the more generalized Bananaquit remained relatively stable in numbers.

Winter resident population fluctuations.—Populations of winter residents fluctuated in the opposite direction of resident bird populations (Fig. 4). The total of resident insectivores (flycatchers and gleaners) and winter residents indicates an almost constant population of insect eating birds. Combining resident flycatchers and gleaners and comparing them with the winter residents is not unreasonable, as several of the winter residents, particularly the American Redstart, also flycatch; some overlap in resource use must occur. (Adding the partially insectivorous Bananaquit to

this group would give combined densities of 121, 96, 97 and 87 for 1973–1976, a particularly stable figure for the last 3 years when nectarivory could not have been a major factor for the Bananaquit.)

Numbers of the five dominant winter resident species (Parula Warbler, Prairie Warbler, Black-and-white Warbler, American Redstart and Ovenbird) fluctuated considerably from year to year. During the last 2 years of the study when resident populations were lowest, five more species were netted. While the Prothonotary Warbler, Hooded Warbler and Northern Waterthrush were netted only once, 10 Cape May Warblers were caught in 1975 and 1976 and five Indigo Buntings were captured in 1976. Neither of these species had been previously seen in the Guanica Forest.

DISCUSSION

With the observation that most Puerto Rican birds breed during the May–June rainy season, it is not difficult to see how lack of rainfall during the first half of the year could drastically affect breeding success and thus population levels. The occurrence of autumn rainfall, even if heavy, may be of relatively little consequence if breeding season conditions are poor. Of course, an extended dry season can have an effect on survivorship, but good conditions in autumn will not help recruitment to the population.

The data suggest that the insectivorous guilds, particularly gleaning insectivores, are least affected by drought conditions, while the frugivores, although able to attain high densities in good conditions, are very sensitive to drought. This difference could be explained by the resources involved. Frugivores feed upon what is basically the yield of primary productivity; with the absence of water there is probably an almost immediate decline in the amount of fruit and seeds produced. In contrast, insectivores feed upon the yield of secondary productivity; even in years when few seeds are produced there are leaves on which insects can feed. Insects may emerge from pupae or hatch in dry conditions following favorable periods and they may linger after conditions become unfavorable. While little is known about island insect densities (Janzen 1973), during the dry season in Costa Rica even the driest locations maintained moderate densities of insects (Janzen and Schoener 1968). Thus, although insects may be relatively scarce, they may be somewhat buffered from climatic fluctuations and birds feeding on insects may show more stable populations than frugivores or nectarivores.

This difference between fluctuations in insectivorous and non-insectivorous guilds has been used to explain the almost total dominance of gleaning insectivores among winter resident species (Faaborg and Terborgh 1980). A bird population attempting to winter within the confines of an island must have a predictable resource. While the availability of fruits,

seeds and flowers may be too variable, the insect resource is stable enough to support winter residents.

Variations in the time required by the different resources to respond to the onset of the wet season could accentuate the differences between guild characteristics. While many plants may flower and fruit rather rapidly after rains (often using stored energy), many insects may require a longer period of time to go through life-cycles and achieve larger sizes and higher densities. Janzen and Schoener (1968) found reduced proportions of subadult insects in the driest sites sampled during the dry season in Costa Rica. Fewer young insects during this period must delay insect population growth during favorable conditions.

The above climatic and resource patterns suggest that it might be best to breed later in the year as rains are then more predictable. This may not be possible due to the high densities of winter resident insect gleaners that arrive in September. Attempting to compete with these winter residents and breed may be impossible, so residents must use the early wet period when conditions are more variable but competition is reduced (see Keast and Morton [1980] for more evidence of this type). Following this logic, frugivores and nectarivores should not be as constrained and the data from Wetmore (1916) suggest this is so. The extent to which these latter species feed insects to their young may put some constraints on their breeding season. A final complexity to the above situation is added by the fact that three other insectivorous species (the Black-whiskered Vireo [*Vireo altiloquus*], Yellow-billed Cuckoo [*Coccyzus americanus*] and Common Nighthawk [*Chordeiles minor*]) breed in the Guanica Forest at the same time as the permanent residents. This complex set of seasonal movements suggests many interesting questions, but more data on resource distributions, philopatry of migrants, and other factors will be needed before any answers can be offered.

Although many resident species declined sharply, no regular member of the Guanica Forest bird community disappeared during this drought. So, while the above data show some interesting responses to severe conditions, this "ecological crunch" was not sufficiently severe to cause even the local extinction of a regular community member. Perhaps it is the occurrence of droughts and other climatic variations such as this or worse that (1) has selected for the proper family composition on these islands (Terborgh 1973), (2) has dictated a level of species saturation in each habitat (Terborgh and Faaborg 1980) and (3) has resulted in rules for structuring the guilds composing these communities (Faaborg 1982). In view of the presumed antiquity of most Puerto Rican residents, it would have been surprising to find local extirpation caused by a 3-year drought. A few uncommon species that are common in other habitats on the island (Puerto

Rican Emerald, Stripe-headed Tanager) did seemingly disappear, but it appears that previous climatic and resource factors have selected a set of species that can coexist through these stress periods when resources are limited and competition is important (Wiens 1977, MacArthur 1972:21). During more favorable conditions, each species may increase in density in response to the types of resources it best uses, probably with less interaction with other community members. During these periods species from other habitats may temporarily invade the Guanica Forest and winter residents may face increased competition from resident insectivores. The members of this community seem well adapted to such severe conditions, thus island turnover must in fact be a rare event in the West Indies.

SUMMARY

The fluctuations of a Puerto Rican dry forest bird population were sampled by netting over a 5-year period that included drought conditions. The absence of normal May and June rains most affected the resident bird populations that breed during this period. Frugivorous species declined most sharply, while gleaning insectivores declined least. Winter resident gleaning insectivores actually increased as resident insectivores declined. It is suggested that insects may provide a scarce, but predictable, resource that attracts winter residents, and thus, in turn, restricts the breeding season of resident insectivores. Such restriction exposes breeding birds to variable early wet season conditions. The relative unpredictability of the fruit, seed and flower resource seems to limit winter residents that use these foods and releases resident members of these guilds from some of the restrictions in breeding. Despite pronounced population declines, no regular member of the Guanica Forest bird community disappeared during the drought.

ACKNOWLEDGMENTS

Financial support for visits to the Guanica Forest was provided by the Frank M. Chapman Fund of the American Museum of Natural History, the Research Council of the Graduate School, University of Missouri–Columbia, and an NSF pre-doctoral grant. I thank Jose Colon of the U.S. Weather Bureau, San Juan, Puerto Rico, for providing rainfall data. The Puerto Rican Department of Natural Resources kindly gave permission and support for the research. James Bond, Joe Wright, Wayne Arendt, Janice Winters, James Karr and Cameron Kepler all made comments on versions of the manuscript.

LITERATURE CITED

Bond, J. 1943. Nidification of the passerine birds of Hispaniola. Wilson Bull. 55:115–125.

———. 1971. Birds of the West Indies, Houghton-Mifflin, Boston, Massachusetts.

Calvesbert, R. J. 1970. Climate of Puerto Rico and U.S. Virgin Islands. Climatography of the United States No. 60–52. U.S. Govt. Printing Office, Washington, D.C.

Diamond, J. M. 1971. Comparison of faunal equilibrium turnover rates on a tropical island and a temperate island. Proc. Natl. Acad. Sci. 68:2742–2745.

——— and R. M. May. 1977. Species turnover rates on islands: dependence on census interval. Science 197:266–270.

Faaborg, J. R. 1982. Trophic and size structure of West Indian bird communities. Proc. Natl. Acad. Sci. USA 1979. In Press.

——— AND J. E. WINTERS. 1979. Winter resident returns and longevity and weights of Puerto Rican birds. Bird-Banding 50:216–223.

——— AND J. E. TERBORGH. 1980. Patterns of migration in the West Indies. Pp. 157–163 *in* Migrant birds in the neotropics: ecology, behavior, distribution, and conservation (A. Keast and E. S. Morton, eds.). Smithson. Inst. Press, Washington, D.C.

——— AND J. E. WINTERS. 1980. More returns from the Guanica Forest, Puerto Rico. J. Field Ornith. 51:368.

JANZEN, D. H. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology 54:687–708.

——— AND T. W. SCHOENER. 1968. Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. Ecology 49:96–110.

KARR, J. R., D. W. SCHEMSKE AND N. BROKAW. 1982. Temporal variation in the understory bird community of a tropical forest. *In* Seasonal rhythms in a tropical forest (E. G. Leigh and A. S. Rand, eds.). Smithson. Inst. Press, Washington, D.C. In Press.

KEAST, A. AND E. S. MORTON. (EDS.) 1980. Migrant birds in the neotropics: ecology, behavior, distribution, and conservation. Smithson. Inst. Press, Washington, D.C.

LYNCH, J. F. AND N. K. JOHNSON. 1974. Turnover and equilibria in insular avifaunas, with special reference to the California Channel Islands. Condor 76:370–384.

MACARTHUR, R. H. 1972. Geographical ecology. Harper and Row, New York, New York.

TERBORGH, J. 1973. Chance, habitat and dispersal in the distribution of birds in the West Indies. Evolution 27:338–349.

——— AND J. FAABORG. 1973. Turnover and ecological release in the avifauna of Mona Island, Puerto Rico. Auk 90:759–779.

——— AND ———. 1980. Saturation of bird communities in the West Indies. Am. Nat. 116:178–195.

WETMORE, A. 1916. Birds of Porto Rico. U.S. Dept. Agric. Bull. 326.

WIENS, J. A. 1977. On competition and variable environments. Am. Sci. 65:590–597.

WILLIS, E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panama. Ecol. Monogr. 44:153–169.

DIVISION OF BIOLOGICAL SCIENCES, UNIV. MISSOURI-COLUMBIA, COLUMBIA, MISSOURI 65211. ACCEPTED 25 APR. 1981.

Appendix

Two-day Capture Totals by Species and Guild for the Combined 32 Nets 1973–1976 and the 16 Net Line 1972–1976 (in parentheses)[a]

Species	$\bar{x}$ weight (g)	Yearly captures				
		1972	1973	1974	1975	1976
Frugivores						
Zenaida Dove (*Zenaida aurita*)	153.0	—	—	1 (1)	—	—
Common Ground Dove (*Columbina passerina*)	35.4	(5)	54 (40)	2 (1)	7 (2)	14 (10)
Northern Mockingbird (*Mimus polyglottos*)	43.8	—	1 (1)	—	—	—
Pearly-eyed Thrasher (*Margarops fuscatus*)	100.7	(4)	3 (1)	5	9 (1)	10 (5)
Red-legged Thrush (*Mimocichla plumbea*)	74.5	(4)	2 (1)	5 (3)	8 (3)	—
Blue-hooded Euphonia (*Euphonia musica*)	15.7	—	—	—	—	1
Stripe-headed Tanager (*Spindalis zena*)	29.7	—	7 (2)	1	—	—
Puerto Rican Bullfinch (*Loxigilla portoricensis*)	32.1	(27)	49 (36)	16 (12)	15 (7)	8 (2)
Black-faced Grassquit (*Tiaris bicolor*)	9.7	(10)	29 (24)	6 (6)	11 (11)	15 (14)
Yellow-faced Grassquit (*Tiaris olivacea*)	7.0	—	—	—	—	1 (1)
Total frugivores	—	(50)	145 (105)	36 (23)	50 (24)	49 (32)
Flycatching insectivores						
Puerto Rican Tody (*Todus mexicanus*)	5.4	(3)	12 (6)	5 (1)	2 (1)	2 (1)
Stolid Flycatcher (*Myiarchus stolidus*)	22.9	(14)	18 (13)	10 (5)	19 (12)	21 (10)
Caribbean Elaenia (*Elaenia martinica*)	22.0	—	—	—	1 (1)	—
Grey Kingbird (*Tyrannus dominicensis*)	47.6	—	—	—	1 (1)	—
Total flycatchers	—	(17)	30 (19)	15 (6)	23 (15)	23 (11)
Gleaning insectivores						
Puerto Rican Lizard Cuckoo (*Saurothera vieilloti*)	77.1	—	2 (1)	—	—	1 (1)

Appendix
Continued[a]

Species	$\bar{x}$ weight (g)	Yearly captures 1972	1973	1974	1975	1976
Puerto Rican Vireo (*Vireo latimeri*)	11.2	—	7 (3)	2	2 (1)	—
Adelaide's Warbler (*Dendroica adelaidae*)	6.7	(3)	7 (5)	9 (4)	3 (2)	3
Black-cowled Oriole (*Icterus dominicensis*)	37.2	—	1	1	2	—
Troupial (*Icterus icterus*)	72.2	(3)	4 (2)	2 (2)	8 (6)	4 (4)
Total gleaning insectivores	—	(6)	21 (11)	14 (6)	15 (9)	8 (7)
Nectarivores						
Puerto Rican Emerald (*Chlorostilbon maugaeus*)	2.8	(1)	—	—	—	—
Antillean Mango (*Anthracothorax dominicus*)	5.4	(8)	11 (8)	6 (5)	2 (2)	2 (2)
Bananaquit (*Coereba flaveola*)	9.4	(21)	55 (13)	34 (8)	36 (21)	21 (12)
Total nectarivores	—	(30)	66 (21)	40 (13)	38 (23)	23 (14)
Winter residents						
Black-and-white Warbler (*Mniotilta varia*)	9.7	(5)	6 (2)	7 (2)	2	4
Prothonotary Warbler (*Protonotaria citrea*)	13.0	—	—	—	—	1
Parula Warbler (*Parula americana*)	7.4	(2)	—	5	4 (1)	8 (1)
Cape May Warbler (*Dendroica tigrina*)	10.0	—	—	—	7	3
Prairie Warbler (*D. discolor*)	6.9	(3)	2 (2)	11 (4)	7 (5)	6 (4)
Ovenbird (*Seiurus aurocapillus*)	18.7	—	2	3	1	1
Northern Waterthrush (*S. noveboracensis*)	15.0	—	—	—	—	1 (1)
Hooded Warbler (*Wilsonia citrina*)	11.0	—	—	—	1	—
American Redstart (*Setophaga ruticilla*)	7.2	(1)	5	7	1 (1)	6
Indigo Bunting (*Passerina cyanea*)	13.2	—	—	—	—	5 (5)
Total winter residents	—	(11)	15 (4)	33 (6)	23 (7)	35 (11)
Total captures	—	(114)	277 (160)	138 (54)	149 (78)	138 (75)

[a] Nomenclature is from Bond (1971) and weights are from Faaborg and Winters (1979) who list statistical data.

Wilson Bull., 94(1), 1982, pp. 31–45

NEST-SITES AND HABITAT OF RED-SHOULDERED AND RED-TAILED HAWKS IN IOWA

James C. Bednarz and James J. Dinsmore

Numerous studies have addressed the breeding biology of the Red-tailed Hawk (*Buteo jamaicensis*) (referred to as RTH) (e.g., Fitch et al. 1946, Orians and Kuhlman 1956, Luttich et al. 1971, Seidensticker and Reynolds 1971, Gates 1972, McInvaille and Keith 1974, Johnson 1975, Petersen 1979), and the Red-shouldered Hawk (*B. lineatus*) (referred to as RSH) (Stewart 1949, Henny et al. 1973, Wiley 1975, Portnoy and Dodge 1979). However, only a few studies (Campbell 1975, Howell et al. 1978) have quantified some parameters of nesting habitats of RSH and RTH. Recently, Titus and Mosher (1981) quantitatively examined the nest-sites of four sympatric woodland hawks (including RSH and RTH) in the central Appalachians. Here we describe nest-sites and examine habitat partitioning of nesting RSH and RTH in Iowa.

STUDY AREA AND METHODS

Fieldwork was done during the spring and summer of 1977 and 1978. Most nests studied were in northeastern Iowa, but data also were collected from four RTH nest-sites in central Iowa. Intensive agriculture (corn, soybeans, cattle feedlots) is the dominant land use in both areas. Most hawk nests were along rivers and streams where cropland interdigitated with woodland and pasture. This land has steep topography or intermittently flooded bottomlands and is unsuitable for row crops. Nest searches following the methods of Craighead and Craighead (1956) were done in both forested bottomlands and upland habitats. All RSH nests found were in floodplain forests dominated by silver maple (*Acer saccharinum*), American elm (*Ulmus americana*) and cottonwood (*Populus deltoides*). Red-tailed Hawk nests were found both in floodplains and upland oak (*Quercus* sp.)-hickory (*Carya* sp.) communities.

Nest tree height and nest height were measured with a rangefinder. Slope of ground supporting the nest tree was determined with an oblique distance pendulum. Diameter of branches supporting nests and nest diameter were recorded for 22 nests climbed in 1978 and two 1977 RSH nests.

The quadrat and point-centered quarter methods were used to quantify vegetation at 38 nest-sites (Mueller-Dombois and Ellenberg 1974). Quadrats consisted of a 730-m^2 circle (radius = 15.24 m) centered on the nest tree. Four 64-m point-quarter transects following the cardinal directions were run from each nest tree. Twenty-nine points were sampled at each nest-site; one at the nest tree and seven (spaced 9.14 m) on each transect. If the transect entered a clearing, point-quarter transects were continued only to the last point where trees could be measured. Diameter at breast height (dbh) was measured and tree density was calculated for all trees greater than 5 cm dbh. These measures are referred to as quadrat dbh, quadrat density, point dbh and point density.

Other variables examined in the nest-site analysis were (1) tree-nest difference—nest tree height minus nest height in meters, (2) slope aspect—direction exposure of slope (N, NE, E, SE, S, SW, W, NW), (3) nest location—on main trunk crotch, on principal branch crotch, braced

against trunk with smaller branches, leaning straight branch, or overhanging branch (crotch—a vertically oriented three or more branch juncture on the main trunk or principal branch capable of supporting a buteo nest), (4) nest-trunk difference—distance between nest and main trunk estimated in meters, (5) branch class—number of branches supporting nest with diameter ≤5 cm (A), >5 cm but ≤10 cm (B), or >10 cm (C) (estimated from ground), (6) canopy cover—canopy cover at nest height in percent (estimated: 0, 5, 10, 20, 30, 40, or 50%), (7) mean nest diameter—(longest + shortest diameter)/2 in meters, (8) mean support branch diameter—mean diameter of branches supporting nest in cm, (9) woodlot size—nesting woodlot size in ha (determined from a cover map using a planimeter), (10) nest openness—mean arc distance between nest support branches, calculated as (nest circumference − sum of diameters of support branches)/no. of support branches, and (11) tree density at nest height—estimated by using regression analysis to determine the number of trees reaching nest height within each 730-m^2 nest quadrat and recorded as no./ha (see Bednarz 1979).

Data were collected at 26 RTH, and eight active and four inactive (alternate or abandoned) RSH nest-sites. Sample size is not equal for all variables because several nest trees could not be climbed, and one inactive nest blew down before a complete data set was collected. Variables used in the microhabitat nest-site discrimination analysis were nest tree height, tree-nest difference, nest tree dbh, slope, nest location, nest-trunk difference, number of nest support branches, branch class A (percent), branch class B (percent), mean nest diameter, mean supporting branch diameter, nest openness, tree density at nest height, quadrat density, quadrat dbh, and woodlot size.

Cover maps were drawn from 1969–1971 aerial photos at 38 nest-sites. Maps were updated in the field. A compensating polar planimeter was used to measure the areas of cover types within a 1-km radius (314-ha circle) of each nest. Distance of woodland edge along potential nonforested hunting habitat (pastures, marshes, prairie, etc.) was measured with a map measuring wheel. Neither species was observed foraging in cropland and, therefore, this habitat type was not considered potential hunting habitat. The mean maximum diameters of 34 red-shoulder and 16 red-tail ranges were 1.4 and 2.8 km, respectively (calculated from Craighead and Craighead 1956:258–263). Therefore, the 2-km diameter used here should include most of the range used at each nest.

Variables included in the habitat discriminant analysis were upland forest area, marsh area, upland hunting area, number of separate hunting areas, mean size of hunting areas, human use area, cropland area, and edge. Floodplain forest area was negatively correlated with upland forest and cropland and was discarded by the stepwise discriminant procedure.

The data were tested univariately with Student's *t*-tests, chi-square tests, and analysis of variance (Snedecor and Cochran 1967); multivariate analysis of nest-site and habitat data was done with discriminant function and profile analyses (Morrison 1976). Data on slope aspects of nests were tested with the Kolmogorov-Smirnov test. Values presented after means are standard deviations. Computer analyses were done with SAS (Statistical Analysis System, Barr et al. 1976) and BMDP (Biomedical Data Package–1977; Health Sciences Computing Facility, University of California–Los Angeles) program packages.

RESULTS AND DISCUSSION

Nest-sites and nests.—We found 12 Red-shouldered Hawk nests in four different tree species and 24 Red-tailed Hawk nests in nine different tree species. Buteos are thought to select nest trees in relation to the availability of large trees (Dixon 1928, Bent 1937). Howell et al. (1978) reported that species of nest trees used by RTH were correlated with tree impor-

TABLE 1
COMPARISON OF RED-SHOULDERED AND RED-TAILED HAWK NEST-SITE CHARACTERISTICS

Variable	Red-shouldered Hawk N	Red-shouldered Hawk Mean ± SD	Red-tailed Hawk N	Red-tailed Hawk Mean ± SD	Probability[a]
Nest height (m)	11	19.1 ± 4.8	26	17.1 ± 4.2	0.2035
Nest tree height (m)	12	28.6 ± 4.6	26	22.1 ± 5.1	0.0006**
Tree–nest difference (m)	11	9.2 ± 1.9	26	5.0 ± 3.0	<0.0001**
Nest tree dbh (cm)	12	63.0 ± 12.7	26	48.9 ± 12.9	0.0031*
No. of support branches	11	3.6 ± 0.5	27	3.7 ± 1.3	0.6891
Nest–trunk difference (m)	11	0.3 ± 0.8	26	0.7 ± 1.2	0.2381
Canopy cover (%)	12	27.5 ± 12.9	26	12.2 ± 11.8	0.0009**
Mean supporting branch diameter (cm)	7	17.2 ± 6.6	18	8.9 ± 3.0	0.0126*
Mean nest diameter (cm)	7	57.1 ± 8.4	17	68.2 ± 10.0	0.0169*
Nest openness (cm)	7	33.8 ± 9.0	17	55.6 ± 14.7	0.0015*
Slope (degrees)	12	0.1 ± 0.3	26	17.2 ± 12.3	<0.0001**
Tree density at nest height (#/ha)	11	161.9 ± 68.1	26	118.7 ± 71.1	0.0961

[a] Student's *t*-test.
* Significant ($P < 0.05$); ** significant ($P < 0.001$).

tance values (sum of relative density, the relative frequency and the relative basal area). Perusal of 44 papers on nesting RSH revealed that 40 species have been used as nest trees, suggesting that species is relatively unimportant in nest-site selection.

RTH nests typically were in smaller trees, closer to the tops of trees, in areas of less canopy cover, had greater nest openness, and more often were placed in trees on slopes than RSH nests (Table 1). Nest openness of only three RTH nests overlapped the range of RSH. Two of these nests were unsuccessful; one had been deserted for several days preceding measurement, and had weathered. The nest openness of the successful nest was only 0.02 cm smaller than the largest RSH nest. By placing their nests high in trees on slopes, RTH in Iowa may have improved access because the canopy of trees downslope of the nest does not reach nest height. Although the limited number of trees on level ground may force many Iowa RTH to nest on forested slopes, all nests on slopes we examined had at least some nesting trees on near-level ground available nearby.

RTH nests are larger than RSH nests, but are located on smaller support branches (Table 1). RSH located their nests either on a main trunk crotch (86%) or on a main branch crotch (14%). RTH constructed nests in all locations (see Methods), most commonly braced by small branches against the main trunk (38%). The tendency for RSH to place nests on a main

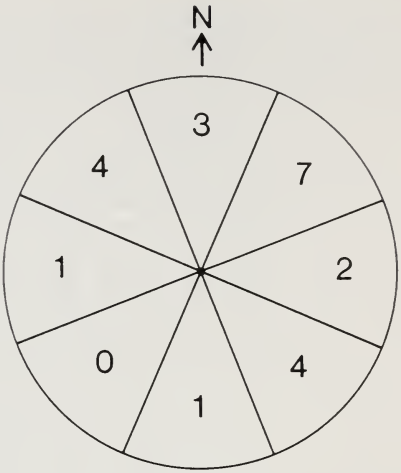


FIG. 1. Direction aspect of 22 Iowa Red-tailed Hawk nests located on hillsides.

trunk crotch more often than RTH was significant ($\chi^2 = 8.6$, df = 1, $P < 0.01$). Previous workers also noted that red-shoulders primarily built nests in secure tree crotches (Bent 1937, Stewart 1949).

Most streams in the study area drain to the southeast. Therefore, most available slope aspects are northeast and southwest. RTH tended to avoid placing nests on southwest facing slopes (Fig. 1), but this result was not significant ($P = 0.17$, Kolmogorov-Smirnov test), possibly because of small sample size. In addition, the single nests located on west and south facing slopes were unsuccessful. Hawk nests on southwest facing slopes are exposed to higher temperatures and greater insolation (Geiger 1965:369–393), perhaps causing heat stress in the young. Mosher and White (1976) thought that Golden Eagles (*Aquila chrysaetos*) selected cliff nests oriented to reduce direct insolation and thermal stress.

The two hawk species differed significantly in four general habitat features (Table 2). RSH were associated with large woodlots and built their nest close to water, but seemed to avoid buildings and roads. We believe that woodlot size is the most important variable. Many workers have reported that RSH nest primarily in larger woodlots (Bent 1937, Stewart 1949, Henny et al. 1973, Campbell 1975). Conversely, RTH generally inhabit more open habitats and will nest in fencerows or isolated trees (Hagar 1957, Bock and Lepthien 1976).

RSH often are associated with open water (Hahn 1927, Dixon 1928, Wiley 1975, Titus and Mosher 1981). This species probably is not depen-

TABLE 2

COMPARISON OF RED-SHOULDERED AND RED-TAILED HAWK NEST LOCATIONS IN RELATION TO WOODLOT SIZE AND DISTANCE TO NEAREST WATER, BUILDINGS AND ROADS

Variable	Red-shouldered Hawk		Red-tailed Hawk		Probability of a larger t value[a]
	N	Mean ± SD	N	Mean ± SD	
Woodlot size (ha)	12	98 ± 65	26	47 ± 44	0.0076*
Distance to water (m)	12	142 ± 120	26	522 ± 571	0.0030*
Distance to road (m)	12	820 ± 509	26	309 ± 233	0.0054*
Distance to building (m)	12	1001 ± 510	26	495 ± 218	0.0058*

[a] Student's t-test.
* Signficant ($P < 0.05$).

dent on water per se, but rather, is adapted to the forested floodplain consisting of level woodlands interspersed with small marshes and backwater channels created by flowing water.

RTH nested closer to buildings and roads than did red-shoulders (Table 2). This seems a consequence of the habitat in Iowa. RTH primarily used open farmland areas which are associated with roads and buildings; RSH were found in the bottomland habitats of wildlife refuges and parks with few roads and buildings. Campbell (1975) found RSH nesting in woodlots near busy highways and ongoing land-development projects.

The discriminant analysis of 13 variables that exhibited differences or represented important characteristics of the nest-site microhabitat (see Methods) correctly classified all 37 nest-sites to the proper species (Fig. 2).

Mean nest diameter, mean supporting branch diameter and nest openness were recorded at only 23 of the 37 nest-sites and could not be included in the analysis of the total sample. These three variables were included in a second discriminant analysis with a smaller sample. Branch classes A and B were deleted from the second analysis because they duplicated the variable mean supporting branch diameter. Again, all nest-sites were properly classified (Fig. 3). The single RSH outlier had the largest nest openness and the greatest mean supporting branch diameter (Fig. 3).

For each analysis, the six variables with the best discrimination power, ranked according to the discriminant coefficients, generally are related directly to nest accessibility (Table 3).

Natural selection of a species' nest-site preference is related to many factors such as providing safety from predators and weather, adequate access to nest, proper support, site availability and adequate area for adults and young. This study shows that red-tail nests are characterized

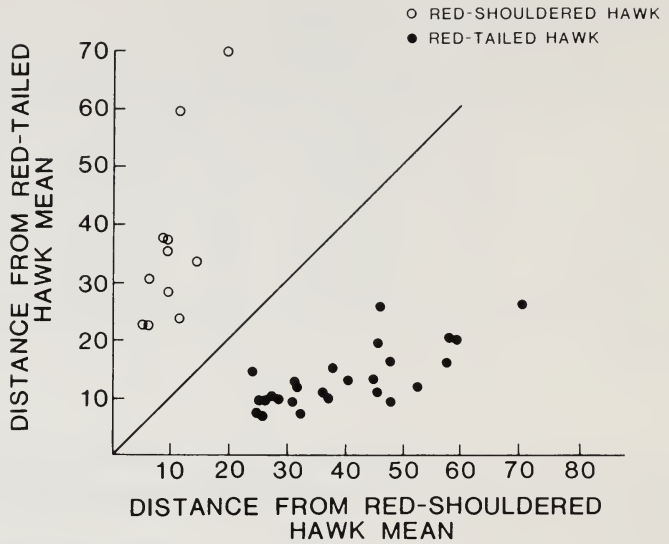


FIG. 2. Discriminant analysis of 11 Red-shouldered and 26 Red-tailed hawk nest-sites graphically represented by Mahalanobis distances from the respective means.

FIG. 3. Discriminant analysis of seven Red-shouldered and 16 Red-tailed hawk nest-sites graphically represented by Mahalanobis distances from the respective means.

TABLE 3

THE SIX MOST IMPORTANT VARIABLES IN THE CLASSIFICATION OF RED-SHOULDERED AND RED-TAILED HAWK NEST-SITES RANKED ACCORDING TO DISCRIMINANT COEFFICIENTS

Discriminant analysis of 37 nest-sites		Discriminant analysis of 23 nest-sites	
Variable	Discriminant coefficient	Variable	Discriminant coefficient
Slope	0.78	Quadrat density	1.30
Tree density at nest height	0.63	Nest openness	1.20
Nest location	0.52	Slope	1.14
Tree–nest difference	0.50	No. of support branches	1.06
Quadrat density	0.38	Quadrat dbh	0.97
Nest tree height	0.37	Tree–nest difference	0.81

by high accessibility. Red-tail nests are built high in trees, on small support branches, located in lower density forests, in areas of less canopy cover and more often in a tree on a slope (Tables 1, 2) than RSH nests. This accessibility makes nests vulnerable to storm damage and increases exposure to direct sunlight and temperature extremes, which can be stressful to young raptors (Mosher and White 1976). Additionally, red-tails construct relatively large nests on small branches (Table 1). We believe it is unlikely that space needed for young has led to the evolution of the present large diameter RTH nest. All RTH nests we examined seemed to provide more than adequate space for the young compared to obviously crowded RSH nests with as many as four young. Alternatively, we suggest that one possible function of the large diameter nest is to improve nest access.

Seemingly, Red-tailed Hawks also increase nest accessibility by placing nests in isolated trees or edge situations (Orians and Kuhlman 1956, Bohm 1978). Mader (1978) suggested that red-tails do not use palo verde (*Cercidium* sp.) and ironwood trees (*Olneya tesota*) often as nest-sites because it is difficult for them to penetrate and construct nests in the dense canopy. Petersen (1979:20) felt that a free avenue of approach was an important factor in RTH nest-site selection. Titus and Mosher (1981) indicated that separating variables in their discriminant analysis of RSH and RTH nest-sites probably represented differences in accessibility. Considering the above, we hypothesize that given a suitable territory the overriding factor in Red-tailed Hawk tree nest-site selection is accessibility to the nest.

Red-shouldered Hawks have proportionately shorter wings and longer tails than RTH (Johnson and Peeters 1963:436), theoretically improving steering ability and maneuverability. Therefore, nest access probably is

TABLE 4

COMPARISON OF MEAN TREE DENSITY AND DBH DETERMINED BY THE QUADRAT AND POINT-QUARTER SAMPLING TECHNIQUES AT 12 RED-SHOULDERED AND 26 RED-TAILED HAWK NEST-SITES IN IOWA

Variable	Red-shouldered Hawk mean ± SD	Red-tailed Hawk mean ± SD	Probability[a]
Quadrat density (number of trees/ha)	643.0 ± 236.0	473.0 ± 216.0	0.0347*
Point density (number of trees/ha)	591.1 ± 193.0	393.0 ± 197.0	0.0065*
Quadrat dbh (cm)	21.5 ± 4.8	20.9 ± 6.4	0.7822
Point dbh (cm)	22.6 ± 4.3	22.7 ± 6.3	0.9641

[a] Student's *t*-test.
* Significant ($P < 0.05$).

less important, and red-shoulders are able to use nests lower in the canopy and with larger support branches, thereby protecting their young from insolation and adverse weather.

Nest-site vegetation.—Analysis of variance was used to test if differences in tree dbh or tree density existed among the seven points along the point-quarter transects extending from the nest-sites of each species. These analyses showed that tree dbh ($P > 0.1$) and tree density ($P > 0.1$) did not differ along the 64-m radii extending from the nest trees of either species.

The woodlots used by nesting RSH had greater tree densities than those used by nesting RTH (Table 4). This supports the hypothesis that RTH only used nest-sites with high accessibility. Selective cutting in dense woodlots could possibly open habitats currently used only by RSH to competition with RTH.

The mean dbh of trees around the nest-sites of both species were nearly identical (Table 4). However, Red-shouldered Hawks tended to nest in woodlots with more large canopy trees and fewer subcanopy ones than found in RTH nesting woodlots (Fig. 4). The difference was significant for quadrat data ($\chi^2 = 11.7$, df = 3, $P = 0.0086$), but not for the point-quarter data ($\chi^2 = 7.5$, df = 3, $P = 0.057$). Perhaps RSH, which commonly fly below the canopy (Bent 1937, Stewart 1943, Johnson and Peeters 1963, pers. obs.), selected woodlands with a larger proportion of canopy trees and thereby had fewer obstructions from small and middle-sized trees.

Mean tree density and dbh did not differ significantly ($P > 0.1$) between the two sampling techniques (Table 4). The point-quarter method tends to underestimate density when aggregated populations are sampled (Risser and Zedler 1968). Therefore, results from the quadrat method were used for the discriminant function analysis of nest-sites.

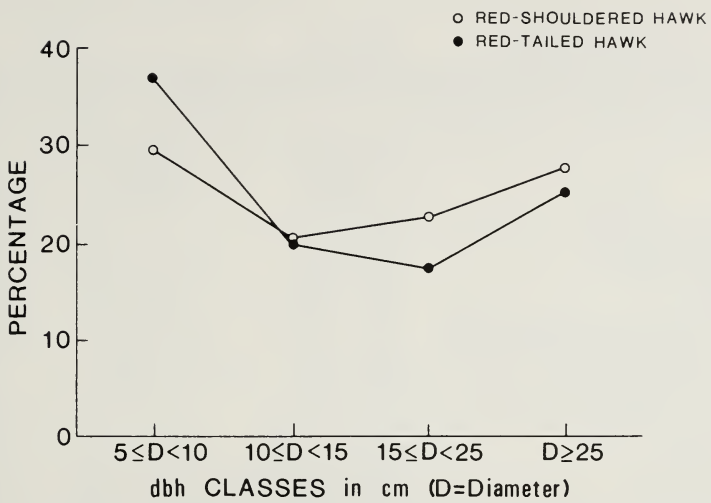


FIG. 4. Percentage of trees in four different dbh classes occurring within a 730-m^2 circular quadrat centered on 12 Red-shouldered and 26 Red-tailed hawk nests.

Nesting habitat.—For both species, hunting area was considered to be nonforested marsh, pasture, or other open area. Breeding RTH primarily hunt in nonforested areas (Smith and Murphy 1973, Howell et al. 1978, Petersen 1979:48). RSH also do much of their hunting in nonforested areas, primarily marshes and wet meadows (Craighead and Craighead 1956, Portnoy 1974, Bednarz 1979:71), although they may also hunt within woodlands.

RSH nesting habitat is characterized by a large area of floodplain forest, numerous small hunting areas, usually marshes and little cropland (Table 5). The large edge distance is an important indicator of this habitat. RTH nesting habitat is characterized by the presence of some upland forest, fewer but larger hunting areas, usually upland areas and a large area of cropland (Table 5).

Discriminant analysis correctly classified all 12 RSH nests and 24 of 26 RTH nests (Fig. 5). The most important variables in this discrimination, ranked according to their discriminant coefficient, were cropland area (1.03), upland forest area (0.88), number of feeding areas (0.63), upland hunting area (0.52) and edge distance (0.49).

Cropland area was by far the most important discriminating variable. As long as adequate hunting area (e.g., pastures) was available, the RTH was able to use agricultural lands. Large areas of cropland on level floodplains usually meant that marshes and forest habitats, important to RSH,

TABLE 5

COMPARISON OF 11 HABITAT PARAMETERS DETERMINED FROM A 1-KM RADIUS CIRCULAR PLOT CENTERED ON RED-SHOULDERED AND RED-TAILED HAWK NESTS IN IOWA

Variable	Red-shouldered Hawk mean ± SD (N = 12)	Red-tailed Hawk mean ± SD (N = 26)	Probability[a]
Floodplain forest (ha)	123.2 ± 75.6	11.3 ± 26.0	0.0003**
Upland forest (ha)	70.0 ± 51.7	92.5 ± 52.2	0.2244
Marsh (ha)	39.3 ± 22.9	5.0 ± 14.2	0.0002**
Upland nonforested hunting area (ha)	19.1 ± 17.4	70.5 ± 20.0	<0.0001**
Total nonforested hunting area (ha)[b]	58.4 ± 26.8	75.4 ± 24.1	0.578
Number of hunting areas	24.6 ± 12.1	14.0 ± 5.2	0.0124*
Mean size of hunting areas (ha)	2.8 ± 1.5	6.4 ± 4.0	0.0003**
Human use area (ha)	2.6 ± 4.2	4.5 ± 4.4	0.2099
Cropland (ha)	17.3 ± 17.1	113.2 ± 53.8	0.0001**
Open water (ha)	40.6 ± 20.5	11.3 ± 20.5	0.0002**
Edge (m)[c]	15,115.0 ± 6497.0	9718.0 ± 3990.0	0.0180*

[a] Student's *t*-test.
[b] Total hunting area includes marsh and upland hunting area.
[c] Edge is distance of forest bordering marsh or upland hunting areas.
* Significant ($P < 0.05$); ** significant ($P < 0.001$).

had been altered. Upland forest area probably was an important variable because it supplied hunting perches and, usually, the nesting area for RTH. Upland forest is probably not necessary for the Red-shouldered Hawk if adequate floodplain forest is available. RSH use of upland forest habitats in Iowa is primarily limited to peripheral areas immediately adjacent to floodplains (Bednarz and Dinsmore 1981). Both RTH and RSH will use and perhaps compete for floodplain forests of limited size, but RTH may avoid using floodplain forest that is surrounded by upland forest.

Upland hunting area was important in discrimination because it was found primarily in RTH habitats while marsh was the primary hunting area of RSH (Table 5).

Edge and number of feeding areas are important to RSH, which use numerous small marshes interspersed with forest (Bednarz and Dinsmore 1981). RTH seemed to prefer larger hunting areas with less interspersion and, hence, less edge (Table 5).

Nest habitat fell into three groups (Fig. 5). Outliers normally were the result of a single high or low value of one variable. The RSH group encircled by a solid line included three nests in a large floodplain forest (comprising 80% or more of the area) with no upland, agricultural land, or human development. Conversely, the RTH group of 20 nesting habitats consisted of a variety of cover types averaging 33% upland forest, 25%

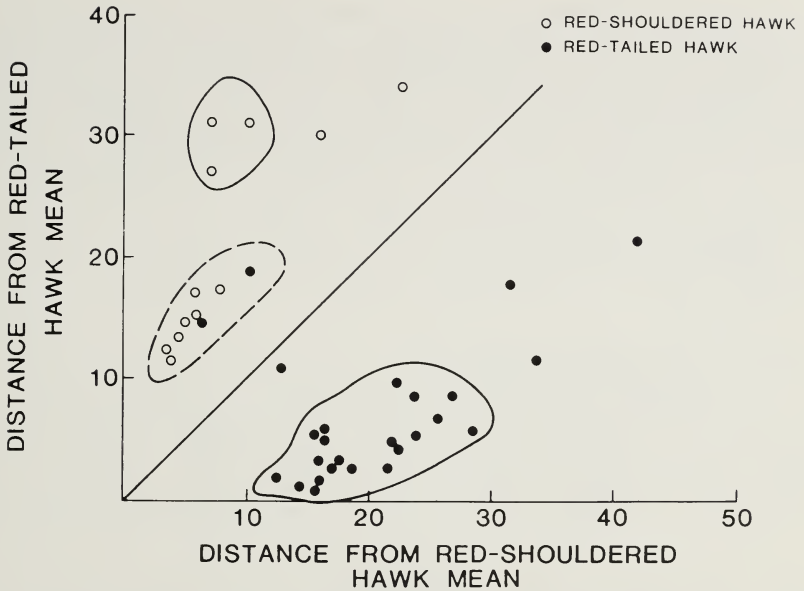


FIG. 5. Discriminant analysis of the habitat surrounding 12 Red-shouldered and 26 Red-tailed hawk nests represented by Mahalanobis distances from the respective means.

pasture or some type of hunting area, 35% cropland, and 7% other land uses, very similar to that described for Alberta (McInvaille and Keith 1974). The third group, within the dashed line, included seven RSH nests plus two RTH nests in floodplains. These habitats averaged 66% forest area (both bottomland and upland), but also included some area in cover types commonly identified with RTH (cropland, upland and human-use areas). This habitat could be considered a transition zone between typical red-shoulder and red-tail habitats which provide enough habitat for Red-shouldered Hawks that hunt within the floodplain forest and associated marsh and backwater areas. The two RTH pairs using this habitat were never seen hunting within the floodplain, but were seen flying to and from adjacent large, open hunting areas.

Nesting RSH generally are associated with extensive forest interspersed with small clearings or wet meadows (Bent 1937, Stewart 1949, Henny et al. 1973, Bednarz and Dinsmore 1981), while nesting RTH are found in open areas and are much less dependent on large woodlands (Fitch et al. 1946, Hagar 1957, Smith and Murphy 1973, Bock and Lepthien 1976, Howell et al. 1978).

Aggressive encounters between RSH and RTH have been reported (Dix-

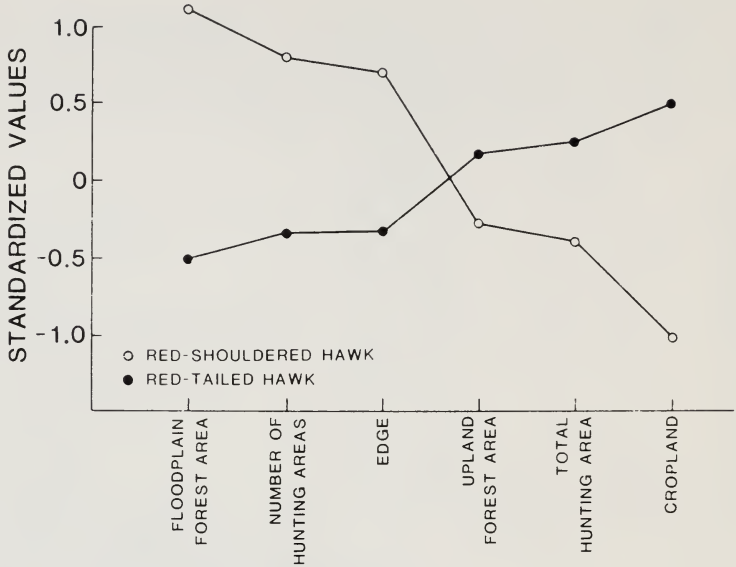


FIG. 6. Nesting habitat profiles of Red-shouldered and Red-tailed hawks in Iowa. Values were standardized by subtracting the mean and dividing by the standard deviation so that values between variables could be compared.

on 1928, Bent 1937, Kilham 1964, Portnoy 1974, Campbell 1975, pers. obs.). Austing (1964) noted that RSH and RTH alternately replaced each other in "fringe" areas. Craighead and Craighead (1956) suggested that RTH nested earlier in the year, and that the number of RSH that were able to nest was dependent on the number of RTH already established. In 6 years, they noted a loss of three RSH pairs and a gain of four RTH pairs occurring simultaneously with draining of swamps, cutting of woodlots and more intensive farming. These observations suggest that these two species compete for nesting areas. We suspect this competition probably is restricted to transitional habitat, and varies regionally. In Iowa, forest clearing and the development of pastures along drainage systems seems to have shifted the competitive advantage from RSH to RTH in bottomland areas. Additionally, the conversion of upland to intensive cultivation (i.e., corn and soybeans) has displaced the RTH and may have encouraged them to compete with RSH for altered habitats along river bottoms. Currently, RTH in Iowa nest extremely close to running water (Roosa 1964), while RSH are restricted to large wooded areas. We consider woodlands averaging 123 ha of floodplain forest and 70 ha of upland forest within 1 km of the nest (Table 5) a minimum size for the red-shoulder in Iowa.

Habitat profiles of six variables showed that Iowa RSH used a large area of floodplain forest, numerous small hunting areas and much edge, while RTH primarily used areas with upland forest along streams, relatively few large hunting areas and a large area of cropland (Fig. 6). A test for parallelism by using profile analysis (Morrison 1976) revealed highly significant differences between species ($F = 13.01$, $P < 0.0001$).

The RTH has been called an edge species (Bock and Lepthien 1976). However, our analysis demonstrates that the RSH occupies habitats with more edge than does the RTH (Table 5 and Fig. 6). The Iowa RTH probably is more accurately described as an openland species that requires perches.

The Red-shouldered Hawk in Iowa is a woodland species. The nest-site, vegetation analysis and nesting habitat all show that RSH typically used dense woodlands (Tables 1, 4, 5). As harvest of midwestern forests continues (Thomson 1980), the Red-shouldered Hawk undoubtedly will lose more of its optimum habitat, allowing competition and replacement by the larger Red-tailed Hawk.

SUMMARY

This study compares nest-site microhabitats and nesting habitats of Red-shouldered and Red-tailed hawks in northeastern and central Iowa. RSH and RTH nest-sites differed significantly in nest tree height; tree-nest height difference, nest tree dbh, canopy cover at nest height, mean support branch diameter, mean nest diameter, mean distance between support branches, slope of ground supporting nest tree, woodlot size, distance to nearest water, distance to nearest road and distance to nearest building. Red-tail nests were characterized by accessibility, being placed high in a tree, on small support branches, in areas of little canopy cover, typically on a hillside and having large distances between support branches. Red-shoulder nests usually had secure support and protection by being placed lower in trees, on large support branches, in areas of greater canopy cover, on level topography and having smaller distances between support branches. Red-shoulders built nests in woodlots with more canopy trees and a greater tree density than woodlots used by red-tails. The area of floodplain forest, marsh, upland nonforested hunting area, cropland, open water, number of hunting areas, mean size of hunting areas and total edge surrounding the nest differed significantly between species. Red-shoulders required large amounts of floodplain forest, edge and numerous small hunting areas. Red-tails typically were found in areas with nearly equal proportions of woodland, pasture and cropland. Logging in floodplain forests may open these areas to encroachment by red-tails and displacement of red-shoulders.

ACKNOWLEDGMENTS

Many individuals contributed to this study. We thank D. Roosa, D. Koenig and V. P. McCrow who provided encouragement, constructive advice and assistance in the field; R. Ervin, J. Wagner, M. Plouffe, P. Bartelt, J. McDonald, J. Schaufenbuel, G. Jones, F. Heinz, R. Renken, E. Johnson, M. Garrett and P. Knight also assisted in the field. R. Dahlgren coordinated the allocation of funding and assisted in other ways. D. Shenk, D. Cox and R. J. Harris assisted with the statistical analysis. K. Bildstein, H. Mueller, E. Klaas, D. Graham and M. Bachmann, reviewed this manuscript. Persons who provided suggestions or assis-

tance in other ways include G. Ackerman, L. Best, B. Commings, B. Frederick, D. Hoffmaster, E. Martin, J. Mount, T. Munson, T. Nigus, B. Ohde, S. Postupalsky, M. Ryan, J. Schaefer, W. Smith, R. Sodja, D. Stauffer and G. A. Thibodeau. Funding was provided by the U.S. Fish and Wildlife Service (Migratory Birds Program) through the Iowa Cooperative Wildlife Research Unit (U.S. Fish and Wildlife Service, Iowa Conservation Commission, Iowa State University, and Wildlife Management Institute, cooperating), the Hawk Mountain Sanctuary Association, and the Iowa Agriculture and Home Economics Experiment Station. This is Journal Paper No. J–9612 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project No. 2170.

LITERATURE CITED

Austing, G. R. 1964. The world of the Red-tailed Hawk. J.B. Lippincott Co., Philadelphia, Pennsylvania.

Barr, A. J., J. H. Goodnight, J. P. Sall and J. T. Helwig. 1976. A user's guide to SAS 76. SAS Institute Inc., Raleigh, North Carolina.

Bednarz, J. C. 1979. I. Productivity, nest sites, and habitat of Red-shouldered and Red-tailed hawks in Iowa. II. Status, habitat utilization, and management of Red-shouldered Hawks in Iowa. M.S. thesis, Iowa State Univ., Ames, Iowa.

——— and J. J. Dinsmore. 1981. Status, habitat utilization, and management of Red-shouldered Hawks in Iowa. J. Wildl. Manage. 45:236–241.

Bent, A. C. 1937. Life histories of North American birds of prey. Pt. 1. U.S. Natl. Mus. Bull. 167.

Bock, C. E. and L. W. Lepthien. 1976. Geographical ecology of the common species of *Buteo* and *Parabuteo* wintering in North America. Condor 78:554–557.

Bohm, R. T. 1978. A study of nesting Red-tailed Hawks in central Minnesota. Loon 50:129–137.

Campbell, C. A. 1975. Ecology and reproduction of Red-shouldered Hawks in the Waterloo region, southern Ontario. Raptor Res. 9:12–17.

Craighead, J. J. and F. C. Craighead, Jr. 1956. Hawks, owls and wildlife. Stackpole Co., Harrisburg, Pennsylvania, and Wildlife Management Inst., Washington, D.C.

Dixon, J. B. 1928. Life history of the Red-bellied Hawk. Condor 30:228–236.

Fitch, H. S., F. Swenson and D. F. Tillotson. 1946. Behavior and food habits of the Red-tailed Hawk. Condor 48:205–237.

Gates, J. M. 1972. Red-tailed Hawk populations and ecology in east-central Wisconsin. Wilson Bull. 84:421–433.

Geiger, R. 1965. The climate near the ground. Harvard Univ. Press. Cambridge, Massachusetts.

Hagar, D. C., Jr. 1957. Nesting populations of Red-tailed Hawks and horned owls in central New York State. Wilson Bull. 69:263–272.

Hahn, W., Jr. 1927. Florida Red-shouldered Hawk. Oologist 44:141–142.

Henny, C. J., F. C. Schmid, E. M. Martin and L. L. Hood. 1973. Territorial behavior, pesticides, and the population ecology of Red-shouldered Hawks in central Maryland, 1943–1971. Ecology 54:545–554.

Howell, J., B. Smith, J. B. Holt, Jr. and D. R. Osborne. 1978. Habitat structure and productivity in Red-tailed Hawks. Bird-Banding 49:162–171.

Johnson, N. K. and H. J. Peeters. 1963. The systematic position of certain hawks in the genus *Buteo*. Auk 80:417–446.

Johnson, S. J. 1975. Productivity of the Red-tailed Hawk in southwestern Montana. Auk 92:732–736.

KILHAM, L. 1964. Interspecific relations of crows and Red-shouldered Hawks in mobbing behavior. Condor 66:247–248.

LUTTICH, S. N., L. B. KEITH AND J. D. STEPHENSON. 1971. Population dynamics of the Red-tailed Hawk (*Buteo jamaicensis*) at Rochester, Alberta. Auk 88:75–87.

MADER, W. J. 1978. A comparative nesting study of Red-tailed Hawks and Harris' Hawks in southern Arizona. Auk 95:327–337.

MCINVAILLE, W. B., JR. AND L. B. KEITH. 1974. Predator-prey relations and breeding biology of the Great Horned Owl and Red-tailed Hawk in central Alberta. Can. Field-Nat. 88:1–20.

MORRISON, D. F. 1976. Multivariate statistical methods. 2nd ed. McGraw-Hill Book Co., New York, New York.

MOSHER, J. A. AND C. M. WHITE. 1976. Directional exposure of Golden Eagle nests. Can. Field-Nat. 90:356–359.

MUELLER-DOMBOIS, D. AND H. ELLENBERG. 1974. Aims and methods of vegetation ecology. John Wiley & Sons, New York, New York.

ORIANS, G. AND F. KUHLMAN. 1956. Red-tailed Hawk and horned owl populations in Wisconsin. Condor 58:371–385.

PETERSEN, L. 1979. Ecology of Great Horned Owls and Red-tailed Hawks in southeastern Wisconsin. Wisconsin Dept. Nat. Resour. Tech. Bull. 111.

PORTNOY, J. W. 1974. Some ecological and behavioral aspects of a nesting population of Red-shouldered Hawks (*Buteo lineatus lineatus*). M.S. thesis, Univ. Massachusetts, Amherst, Massachusetts.

——— AND W. E. DODGE. 1979. Red-shouldered Hawk nesting ecology and behavior. Wilson Bull. 91:104–117.

RISSER, P. G. AND P. H. ZEDLER. 1968. An evaluation of the grassland quarter method. Ecology 49:1006–1009.

ROOSA, D. M. 1964. Nesting of raptors in western Wright County. Iowa Bird Life 34:88–90.

SEIDENSTICKER, J. C., IV, AND V. REYNOLDS, III. 1971. The nesting, reproductive performance and chlorinated hydrocarbon residues in the Red-tailed Hawk and Great Horned Owl in south-central Montana. Wilson Bull. 83:408–418.

SMITH, D. G. AND J. R. MURPHY. 1973. Breeding ecology of raptors in the eastern Great Basin of Utah. Brigham Young Univ. Sci. Bull., Biol. Ser. 18(3):1–76.

SNEDECOR, G. W. AND W. G. COCHRAN. 1967. Statistical methods. 6th ed. Iowa State Univ. Press, Ames, Iowa.

STEWART, C. A. 1943. Nesting of the Red-shouldered Hawk in Sarpy County. Nebraska Bird Rev. 11:25–30.

STEWART, R. E. 1949. Ecology of a nesting Red-shouldered Hawk population. Wilson Bull. 61:26–35.

THOMSON, G. W. 1980. Iowa's disappearing woodlands. Iowa State J. Res. 55:127–140.

TITUS, K. AND J. A. MOSHER. 1981. Nest-site habitat selected by woodland hawks in the central Appalachians. Auk 98:270–281.

WILEY, J. W. 1975. The nesting habitat and reproductive success of Red-tailed Hawks and Red-shouldered Hawks in Orange County, California, 1973. Condor 77:133–139.

DEPT. ANIMAL ECOLOGY, IOWA STATE UNIV., AMES, IOWA 50011. (PRESENT ADDRESS JCB: 3832 GOODRICH NE, ALBUQUERQUE, NEW MEXICO 87110.) ACCEPTED 20 APR. 1981.

Wilson Bull., 94(1), 1982, pp. 46–54

BREEDING BIOLOGY AND DIET OF THE FERRUGINOUS HAWK IN SOUTH DAKOTA

Charles L. Blair and Frank Schitoskey, Jr.

The Ferruginous Hawk (*Buteo regalis*) is the largest North American buteo. It occurs throughout most of the western United States and breeds from Alberta to western Texas and from Washington to Arizona. In this study we investigated the breeding biology of the Ferruginous Hawks in northwest South Dakota, complimenting earlier studies by Weston (1969) in Utah, Olendorff (1973) in Colorado, Howard (1975) in Utah and Idaho, and Lokemoen and Duebbert (1976) in north-central South Dakota.

STUDY AREA AND METHODS

The study area encompassed about 7000 km^2 in northwest South Dakota, including all of Harding County. The area is semi-arid and has a mid-continental climate with long, cold winters and short, warm summers (Spuhler et al. 1971).

Eighty-five percent of Harding County is rangeland dominated by western wheatgrass (*Agropyron smithii*) and needle grass (*Stipa comata*). Sagebrush (*Artemesia* spp.) occurs throughout the area and is widespread in the western third of the county. Small grain crops compose 9% of the area, pastureland and tame hay 3% and woodland 3%. Elevated table lands are dominated by ponderosa pine (*Pinus ponderosa*) savannah, whereas green ash (*Fraxinus pennsylvanicus*), willow (*Salix* spp.) and Siberian elm (*Ulmus pumila*) predominate in riparian areas and ravines.

Two or more biologists conducted a daily census of birds on the study area in 1976 and 1977; Ferruginous Hawk studies began the day the first hawk was sighted. Active nests were located either during aerial surveys at altitudes of 150–175 m, or by ground searches from roads. To reduce the possibility of nest abandonment, nests were approached only after at least one egg hatched. Nests were visited once every 2 days to weigh fledglings and collect pellets. We estimated minimum clutch-size from the number of young and the number of remaining unhatched eggs. A nesting attempt was defined as the presence of at least one egg; a successful nest was one from which one or more young fledged. Density of breeding pairs was determined by dividing the number of pairs present by the total area. Nest-sites were classified according to land surface features, vegetative cover and height.

Pellets and prey remains found at the nest-sites were collected. Pellets were collected from 18 nests in 1976 and 17 nests in 1977. Most pellets obtained were from young birds but we felt that the pellets also reflected the adult diet. Percentage of occurrence was calculated for all prey species.

All nestlings were banded with U.S. Fish and Wildlife Service lock-on leg bands. In 1977, six fledglings were fitted with 25 g radio transmitters attached with temporary backpack harnesses (Dunstan 1972). These birds were located by triangulation from two tower receivers within range of each nest; 2147 triangulation locations were plotted. Maximum area was determined by eliminating the 5% of the points that were farthest from the nest and connecting the new outermost points (Odum and Kuenzler 1955).

RESULTS AND DISCUSSION

Nesting density.—In 1976, 24 pairs of Ferruginous Hawks were observed in the study area; 17 pairs and two unpaired adults were present in 1977. Average distance between active nests was 7.2 km in 1976 and 6.4 km in 1977. Density of breeding pairs was one pair per 292 km^2 in 1976 and one pair per 412 km^2 in 1977.

During the 1976 breeding season six pairs occupying territories in early April did not nest. Three of these pairs contained one bird in immature plumage and one bird in adult plumage. Ferruginous Hawks do not breed until their third or fourth year (Brown and Amadon 1968:629). All pairs observed in 1977 nested.

The density of Ferruginous Hawks observed in this study area was lower than that found by other investigators. Lokemoen and Duebbert (1976) reported one pair of Ferruginous Hawks per 17.4 km^2 in north-central South Dakota, and Weston (1969) found one pair per 39.9 km^2 in Utah. Weston observed one pair for each 18.1 km^2 on a small area within his 1969 study area. Platt (1971) reported a density of one pair per 116 km^2 in Curlew Valley, Utah, and Olendorff (1973) found one pair per 99.9 km^2 on a 2598 km^2 study area in Colorado.

Breeding season chronology.—Ferruginous Hawks were first observed on the study area on 24 March 1976 and 27 March 1977; these dates were verified with data from the daily, year-round avian census conducted on the study area. Courtship and nesting activities began during the first week of April. Data were obtained from 18 nests in 1976 and 17 nests in 1977. Assuming an incubation period of 35 days (Olendorff 1973), the median dates of egg-laying were 21 April 1976 and 19 April 1977. Estimated earliest egg-laying dates were 13 April 1976 and 15 April 1977; latest laying dates were 28 April 1976 and 22 April 1977. Earliest observed hatching dates were 17 May 1976 and 20 May 1977. Latest hatching dates were 1 June 1976 and 27 May 1977. First young were fledged 25 June 1976 and 25 June 1977; latest fledging dates were 12 July 1976 and 10 July 1977.

Ferruginous Hawks in Utah arrived in the nesting area in early March and began laying in late March (Smith and Murphy 1973, Howard 1975). Breeding territories were established at a later date in Harding County, South Dakota than in Colorado (Olendorff 1973) or Utah, but approximately the same time as in north-central South Dakota (Lokemoen and Duebbert 1976).

Nest-sites.—Ferruginous Hawks in Harding County nested on five distinct land surface features: riverbed mounds, river cutbanks, low hills, clay buttes and high vegetated hills. Twenty-one of the active nests (55%) were on clay buttes lacking vegetation. The 35 nests studied were located in unbroken, ungrazed, or lightly grazed prairie or badland areas surround-

ed by prairie. In 1976 an additional nest was located in an alfalfa field. Although Ferruginous Hawks often nest in trees (Olendorff 1973), no active Ferruginous Hawk nests were found in several wooded areas within the study area.

All nests were on the ground. Height of the nest above the surrounding prairie ranged from 0–25 m (mean of 6.1 m in 1976 and 8.6 in 1977). The difference between nest heights for 1976 and 1977 was significant (t = 1.86, df = 34, $P < 0.05$). Selection of ground nesting sites might be influenced by preference for exposed nest-sites. All nest-sites in Harding County enabled birds to view a large area surrounding the nest. Nests situated at high vantage points might allow adults to detect both potential predators and prey from the nest. Judging from the difficulty we had in climbing to them, most nest were relatively secure from ground predators.

Thirty of the 35 nests were located within a strip 25 km wide extending from northwest to southeast through the center of the county. This band corresponded roughly with the greatest concentration of buttes and hills, and composed approximately 35% of the study area. Land use in the northeast portion of the county was dominated by small grain farming which rendered many areas unsuitable for nesting Ferruginous Hawks. In southwestern Harding County, the land surface features most frequently selected as nest-sites were lacking.

Eight of 17 nests used in 1977 were located within 1 km of a nest active in 1976; four of these were on sites used the previous year. Smith and Murphy (1973) reported that Ferruginous Hawks reoccupied the same nest-site for as many as 4 consecutive years.

Nests were constructed primarily from dead vegetation. The outer basal portion of each nest consisted mainly of sagebrush branches up to 2.5 cm in diameter. Barbed wire, baling wire, twine, paper, plastic and dried cow manure were found in a number of nests. Most nest-cups were lined with buffalo grass (*Buchloe dactyloides*) and a few pieces of paper and dried manure. Nest size averaged 31 cm high, 121 cm across and 58 cm in nest-cup diameter.

Productivity.—Seventy-two percent of 18 nesting attempts were successful in 1976; 82% of 17 attempts were successful in 1977. Hatching and fledging success are shown in Table 1.

One of five nest failures in 1976 occurred when adults abandoned the nest about 25 days after incubation began. Mammalian predators were responsible for three of the five nest failures in 1976 and one of three failures in 1977. Eight of 11 unhatched eggs were infertile.

In two broods the youngest bird disappeared at about 14 days of age. The first nestling that disappeared weighed 55 g at hatching; its nest mates at that time weighed 75 g, 127 g and 155 g. Two days before it disappeared,

TABLE 1
HATCHING AND FLEDGING SUCCESS OF FERRUGINOUS HAWKS IN HARDING COUNTY DURING 1976 AND 1977

Year	Eggs laid	Eggs hatched		Young fledged		Cause of nestling mortality							
						Starvation[a]		Predation		Abandoned		Unknown	
		N	%	N	%	N	%	N	%	N	%	N	%
1976	59	52	(88)	34	(59)	3	(5)	12	(20)	3	(5)	0	—
1977	56	52	(93)	39	(70)	0	—	5	(9)	0	—	8	(14)
Total	115	104	(90)	73	(64)	3	(3)	17	(15)	3	(3)	8	(7)

[a] Possibly due to starvation, sibling competition, physical defects, or disease.

this bird weighed 195 g, while its siblings weighed 380 g, 402 g and 465 g. In the second instance, the nestling weighed 413 g the day before it disappeared; its nest mates weighed 558 g, 573 g and 694 g. Most likely the youngest birds were either killed and eaten by the larger nestlings or died and were then consumed. Ingram (1959) reported that fratricide occurs frequently among buteos.

The four nests destroyed by predators were located on low (<5 m) hills or clay buttes. All of these sites were easily climbed during nest checks. Fresh fox scats were found at three of the four nests, implicating the red fox (*Vulpes fulva*) as the responsible predator. Coyote (*Canis latrans*) scats were found at the fourth nest. No renesting attempts were made during the study.

Plumage type.—Birds of two distinct plumage types were seen on the study area. Of 84 adults, two (2.5%) were dark phase birds and 82 (97.5%) were light phase. This is similar to 3% dark phase birds in Colorado (Olendorff 1973) and 3.5% dark phase birds in Utah and Idaho (Howard 1975).

Diet during the breeding season.—Three hundred forty-two pellets and individual remains of prey animals were collected from 18 nest-sites in 1976, and 348 from 17 nest-sites in 1977. Mammals composed 70% of the prey items, birds 27% and reptiles 3% (Table 2). Remains of thirteen-lined ground squirrels, Western Meadowlarks and white-tailed jackrabbits occurred most frequently in pellets. Eighty-two percent of Western Meadowlarks identified from pellets and prey remains were juveniles. Cameron (1914) and Angell (1969) found that birds taken as prey were primarily recently fledged individuals. Black-tailed jackrabbits were the major food item of Ferruginous Hawks in Utah (Weston 1969, Smith and Murphy 1973). Ground squirrels were most important in Colorado (Olendorff 1973) and South Dakota (Lokemoen and Duebbert 1976). Woffinden and Murphy

Table 2

Number and Percent of Prey Types in the Diet of Ferruginous Hawks in 1976 and 1977

Species	1976		1977		Both years combined	
	N	%	N	%	N	%
Mammals						
Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*)	156	(46)	147	(42)	303	(44)
White-tailed jackrabbit (*Lepus townsendii*)	18	(5)	49	(14)	67	(10)
Northern pocket gopher (*Thomomys talpoides*)	21	(6)	33	(10)	54	(8)
Eastern cottontail (*Sylvilagus floridanus*)	4	(1)	9	(3)	13	(2)
Black-tailed prairie dog (*Cynomys ludovicianus*)	1	tr[a]	6	(2)	7	(1)
Long-tailed weasel (*Mustela frenata*)	0	(0)	3	(1)	3	tr
Deer mouse (*Peromyscus maniculatus*)	1	tr	1	tr	2	tr
Ord kangaroo rat (*Dipodomys ordi*)	1	tr	0	(0)	1	tr
House mouse (*Mus musculus*)	2	(1)	0	(0)	2	tr
Western harvest mouse (*Reithrodontomys megalotis*)	2	(1)	0	(0)	2	tr
Peromyscus spp.	3	(1)	0	(0)	3	tr
Hispid pocket mouse (*Perognathus hispidus*)	16	(5)	5	(1)	21	(3)
Total mammals	229	(66)	256	(73)	485	(70)
Birds						
Western Meadowlark (*Sturnella neglecta*)	91	(27)	71	(20)	162	(24)
Horned Lark (*Eremophila alpestris*)	6	(2)	3	(1)	9	(1)
Chestnut-collared Longspur (*Calcarius ornatus*)	1	tr	0	(0)	1	tr
Gray Partridge (*Perdix perdix*)	1	tr	0	(0)	1	tr

TABLE 2
CONTINUED

Species	1976 N	1976 %	1977 N	1977 %	Both years combined N	Both years combined %
Common Flicker (*Colaptes auratus*)	0	(0)	4	(1)	4	(1)
Sprague's Pipit (*Anthus spragueii*)	0	(0)	3	(1)	3	tr
Lark Bunting (*Calamospiza melanocorys*)	2	(1)	2	(1)	4	(1)
Sparrow (unknown spp.)	3	(1)	0	(0)	3	tr
Total birds	104	(31)	83	(24)	187	(27)
Reptiles						
Western hog-nosed snake (*Heterodon nasicus*)	6	(2)	6	(2)	12	(2)
Gopher snake (*Pituophis melanoleucus*)	2	(1)	2	(1)	4	(1)
Short-horned lizard (*Phrynosoma douglassi*)	1	tr	0	(0)	1	tr
Leopard frog (*Rana pipiens*)	0	(0)	1	tr	1	tr
Total reptiles	9	(3)	9	(3)	18	(3)
Total prey items	342		348		690	

[a] Tr = <1%.

(1977) attributed a decline in Ferruginous Hawks in Utah to a decline in jackrabbits.

Juvenile post-fledging activity.—The senior author spent approximately 600 h observing juvenile post-fledging activity. Dependence of fledglings on the nest-site as a feeding station ceased 2 weeks after fledging. By this time the young had apparently developed the flying and hunting coordination necessary to make them somewhat independent, although several remained dependent on adults for food for up to 4 weeks after fledging. Although young birds were observed hunting during this period, no actual prey captures were observed. Young birds roosted on buttes and hills within the hunting range of their parents.

The maximum area covered by the fledged young increased each week

TABLE 3

MAXIMUM AREA (HA) USED BY RADIO-TAGGED JUVENILE FERRUGINOUS HAWKS AFTER FLEDGING IN 1977

Bird	Sex	Nest #	Weeks after fledging			
			1	2	3	4
1	M	1	82	365	773	776
2	F	1	128	316	454	658
3	F	2	20	71	247	502
4	F	2	29	211	377	794
5	F	3	88	9	19	94
6	F	3	13	8	16	105
$\bar{x} \pm$ SD			60 ± 46.2	163 ± 156.7	314 ± 287.9	488 ± 318.8

(Table 3). Two weeks after fledging one male and one female from the same nest began using a large hill near the nest for perching and did not return to the nest-site. Two other birds expanded the area which they hunted to include several buttes that provided perching sites the second week after leaving the nest. These buttes had been hunted by their parents. During the next 2 weeks the birds shifted to an area from which wild hay had been cut recently. The round bales of hay provided numerous perches, while the short grass made potential prey readily visible to the young birds. A third duo expanded their range away from human activity; they avoided a heavily used highway and ranch buildings.

Loss of radio and visual contact with the birds generally occurred during the fifth week after fledging. Adult Ferruginous Hawks apparently departed by the first week in September, after having been present on the study area for about 5.5 months.

Probable impact of human activity and development.—Ferruginous Hawks are sensitive to human activity and will readily abandon their nests, even after a single human visit, if the eggs are still unhatched (Snow 1974). Activities in the vicinity of a nest, such as plowing and disking, mineral exploration and extraction, or off-road recreational vehicle use can cause nest abandonment. Such activities occurring repeatedly after the young have hatched may keep the attending adults off the nest for long periods of time. Harding County has extensive mineral resources including oil, gas, uranium and coal. The intensification of agriculture, mineral exploration and development, and increased recreational demands of energy related workers will reduce the number of areas of Harding County which are suitable for nesting Ferruginous Hawks. Since Ferruginous Hawks require areas free from human disturbance for nesting, an increase in

human activity will probably lead to a smaller breeding population of this species in this area.

SUMMARY

The density of Ferruginous Hawk pairs in a 7000 km² study area in northwestern South Dakota was one pair per 292 km² in 1976 and one pair per 412 km² in 1977. Thirteen of 18 nesting attempts were successful in 1976; 14 of 17 attempts were successful in 1977. Successful nests were located in unbroken, ungrazed, or lightly grazed prairie. All nest-sites were on the ground surface on riverbed mounds, river cutbanks, low hills, clay buttes, or high vegetated hills. Prey consisted primarily of thirteen-lined ground squirrels, Western Meadowlarks and white-tailed jackrabbits. Young birds returned to the nest to obtain food from the adults and to roost for 2 weeks after fledging; they left the study area during the fifth week after fledging.

ACKNOWLEDGMENTS

We thank Paul A. Vohs for assistance in this study and Henry L. Short, John T. Lokemoen and Duane A. Ashern for comments on early drafts of this manuscript. This study was funded by the U.S. Fish and Wildlife Service, Western Energy and Land Use Team, Coal Project, Contract 14-16-0008-1181.

LITERATURE CITED

Angell, T. 1969. A study of the Ferruginous Hawk: adult and brood behavior. The Living Bird 8:225–241.

Brown, L. H. and D. Amadon. 1968. Eagles, hawks, and falcons of the world. Vol. 2. McGraw-Hill, New York, New York.

Cameron, S. E. 1914. The Ferruginous Rough-Leg in Montana. Auk 31:159–167.

Dunstan, T. C. 1972. A harness for radio-tagging raptorial birds. Inland Bird-Banding News 44:4–8.

Howard, R. P. 1975. Breeding biology of the Ferruginous Hawk in northern Utah and southern Idaho. M.S. thesis, Utah State Univ., Logan, Utah.

Ingram, C. 1959. The importance of juvenile cannibalism in breeding biology of certain birds of prey. Auk 76:218–226.

Lokemoen, J. T. and H. F. Duebbert. 1976. Ferruginous Hawk nesting ecology and raptor populations in northern South Dakota. Condor 78:464–470.

Odum, H. P. and E. J. Kuenzler. 1955. Measurement of territory and home range size in birds. Auk 72:128–137.

Olendorff, R. R. 1973. The ecology of the nesting birds of prey of northeastern Colorado. U.S.I.B.P. Tech. Rept. No. 211. Colorado State Univ., Fort Collins, Colorado.

Platt, J. B. 1971. A survey of nesting hawks, eagles, falcons, and owls in Curlew Valley, Utah. Great Basin Nat. 31:51–65.

Smith, D. and J. R. Murphy. 1973. Breeding ecology of raptors in the eastern Great Basin in Utah. Brigham Young Univ. Sci. Bull. Biol. Ser. 18.

Snow, C. 1974. Habitat management series for unique or endangered species. Ferruginous Hawk Rept. No. 13. Bureau of Land Management.

Spuhler, W., W. F. Lytle and D. Moe. 1971. Climate of South Dakota. South Dakota State Univ., Agric. Exper. Stat. Bull. 582.

Weston, J. B. 1969. Nesting ecology of raptorial birds in central Utah: nesting ecology of

the Ferruginous Hawk *Buteo regalis*. Brigham Young Univ. Sci. Bull. Ser. 10:25–36.

WOFFINDEN, N. D. AND J. R. MURPHY. 1977. Population dynamics of the Ferruginous Hawk during a prey decline. Great Basin Nat. 37:411–425.

SOUTH DAKOTA COOPERATIVE WILDLIFE RESEARCH UNIT, SOUTH DAKOTA STATE UNIV., BROOKINGS, SOUTH DAKOTA 57007. ACCEPTED 6 MAY 1981.

Wilson Bull., 94(1), 1982, pp. 55–63

IMPLICATIONS OF CONSTRUCTION OF A FLOOD CONTROL PROJECT UPON BALD EAGLE NESTING ACTIVITY

Anne E. Shapiro, Frank Montalbano, III, and Doris Mager

Florida is regarded as the most important breeding area for southern Bald Eagles (*Haliaeetus leucocephalus leucocephalus*) (Sprunt 1954, Sprunt et al. 1973, Robertson 1978). Some of the densest breeding concentrations historically occurred along the now heavily urbanized middle Gulf and Atlantic coasts of the peninsula (Robertson 1978). These coastal populations are now greatly depleted or extirpated. Statewide, populations have decreased by at least 50% during the past 30 years (Robertson 1978).

Fifty-four percent of the statewide eagle production between 1972 and 1975 occurred in central Florida (Nesbitt et al. 1976). The Kissimmee Basin area in the grazing and lake country in the interior of this region (Fig. 1) has traditionally supported an important breeding population (Sprunt 1954, Howell and Heinzman 1967). Although that portion of the population associated with the Kissimmee Basin was regarded as stable as recently as the mid-1960's (Howell and Heinzman 1967), Heinzman and Heinzman (1970) reported a disturbing increase in nest desertions within the Lower Kissimmee Basin. This apparent decline in nest activity occurred during construction of a system of flood protection works in the Basin by the U.S. Army Corps of Engineers (Corps).

Nationwide, declines in certain Bald Eagle populations have continued in spite of reductions in chlorinated hydrocarbon pesticide use. Direct loss or deterioration of suitable habitat resulting indirectly from human activity may have replaced pesticide contamination as the major contributing factor in the decline of the southern Bald Eagle (Murphy and Coker 1978, Robertson 1978). Our study was initiated in an effort to ascertain the relationship between project construction and the status of Bald Eagles nesting in the Kissimmee Basin, and to provide a basis for assessment of the potential impact of system restoration on this endangered species.

STUDY AREA

That portion of the Kissimmee Basin in Osceola, Polk, Okeechobee, Highlands and Glades counties (Fig. 1) was selected for study. Orange and Lake counties were omitted because nesting data for the 1970's in these counties were incomplete.

The Kissimmee River drainage basin covers approximately 7700 km^2 in south-central Florida (Fig. 1). Waters rising near Orlando historically moved through a system of major lakes and associated creeks, marshes and sloughs to Lake Kissimmee (Montalbano et al. 1979a). From Lake Kissimmee, waters passed into the mile-wide floodplain and braided river channel

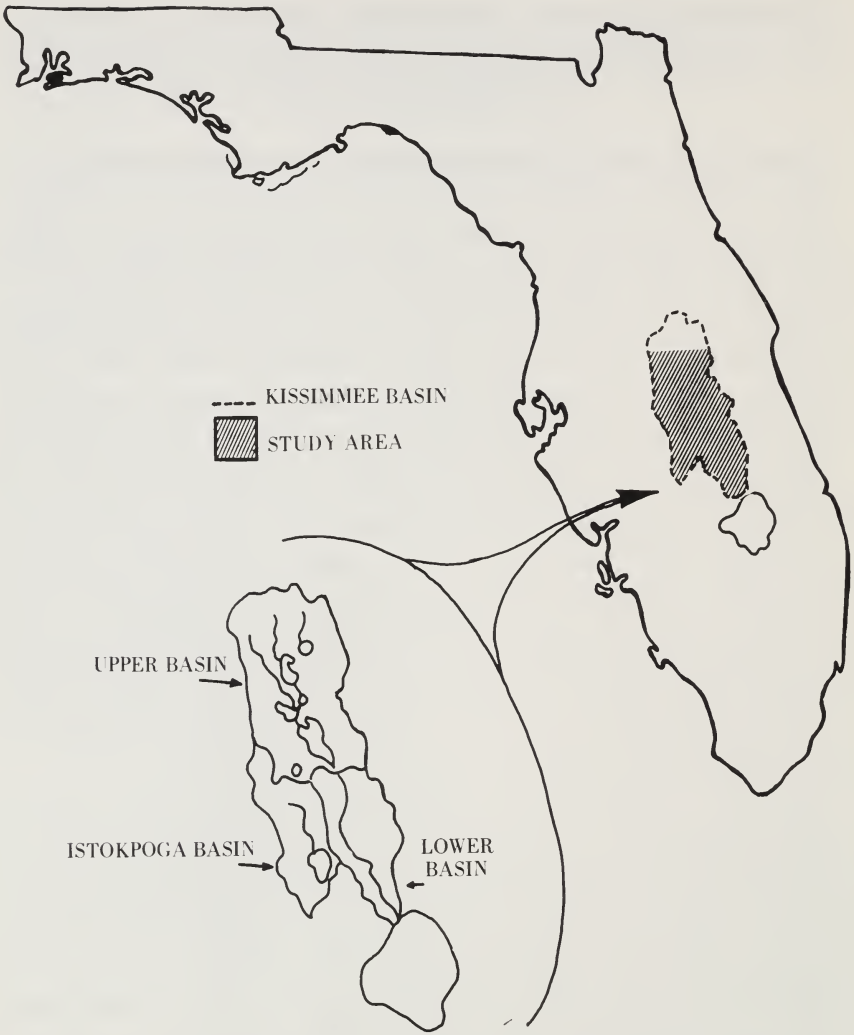


FIG. 1. The Kissimmee Basin, Florida, and location of the study area within this basin.

system of the Kissimmee River enroute to Lake Okeechobee (Florida Department of Administration 1975, Goodrick and Milleson 1974, Montalbano et al. 1979a).

Water level fluctuation was a key element in the productivity of the Kissimmee Basin, contributing to substrate improvement (Wegener and Williams 1974), development of diverse aquatic and wetland plant communities (Goodrick and Milleson 1974, Wegener and Williams 1974) and production and concentration of a high diversity of fish and wildlife food organisms (Burns 1976, Patrick 1978). The Corps completed construction of a flood control system in

the Basin during the 1960's (Florida Department of Administration 1975). This flood control system substantially altered and impaired ecosystem functions in the study area, as discussed below. For the purposes of this study, the Kissimmee River Basin is divided into segments.

Upper Basin.—The Upper Basin is that portion of the study area north of the general route of State Road 60 (Fig. 1). Approximately 13% of this 4100 km² area is covered by surface waters (Heaney et al. 1975), mostly large lakes with extensive littoral zone marshes. As a result of construction of the flood control project, canals between the major lakes of the Upper Basin were enlarged and lake levels were regulated by a system of water control structures completed in 1970 (U.S. Army Corps of Engineers 1979).

Water level stabilization in the Upper Basin reduced lake surface area, intensified agricultural land use and urban development, and resulted in degradation of existing habitat and loss of fishery resources of the area (Wegener and Williams 1975). Waterfowl inventories reported for the period November 1978–March 1979 by Montalbano et al. (1979b) indicated wintering waterfowl populations were approximately 25% below those reported for comparable areas during comparable survey periods between 1954 and 1957 (Florida Game and Fresh Water Fish Commission 1957).

Istokpoga Basin.—The 1700 km² Istokpoga Basin (Fig. 1) includes more than 40 lakes connected by natural streams, creeks, or canals. Lake Istokpoga, the principal lake in the Basin, characteristically fluctuated extensively. High lake stages and the magnitude of fluctuation were initially reduced by the construction of the Istokpoga Canal in 1949, and were further reduced through completion of the authorized flood control system for this portion of the Kissimmee Basin in 1962. Some form of water level management is in effect on most of the lakes in the Istokpoga Basin. High stages have been reduced through modification in outflow capacities, with resulting losses in fish and waterfowl habitats (Milleson 1976).

Lower Basin.—The Lower Basin comprises that portion of the Kissimmee Basin lying south of State Road 60, exclusive of the Istokpoga Basin (Fig. 1). The 1900 km² area (Heaney et al. 1975) includes the channelized Kissimmee River (C–38 Canal) and remnants of the original Kissimmee River and its tributaries.

The excavation of Canal C–38 and the construction of the system of five water control structures along the route of the Kissimmee River in the Lower Basin was completed in 1971 (Goodrick and Milleson 1974, Dineen et al. 1974). The 216-km braided river channel (Montalbano et al. 1979a) was bisected by a 127-km box-sided canal and system of water control structures (Dineen et al. 1974, Goodrick and Milleson 1974). Dredge spoil was deposited on floodplain marshes and in remnants of the braided river channel. Water levels which had fluctuated extensively prior to channelization were stabilized behind the five water control structures (Goodrick and Milleson 1974, Montalbano et al. 1979a). Canal design resulted in permanent drainage of the marshes immediately downstream from each water control structure, and permanent flooding of wetlands upstream from each structure.

MATERIALS AND METHODS

Information on the historical status (1959–1971) of Bald Eagle nesting territories in the Kissimmee River Basin was obtained from the field notes of the late George Heinzman. Heinzman compiled data received from mail surveys conducted in conjunction with the continental Bald Eagle project, and collected data personally on certain nests within the Florida Audubon Society sponsored Kissimmee Cooperative Bald Eagle Sanctuary.

Nesting records for 1972–1979 were obtained from aerial surveys conducted and summarized by D. Mager and T. Hines for the Florida Cooperative Bald Eagle Survey Committee. Flights were initiated in November each year to determine the onset of incubation. A second survey was flown in February to obtain production data. We mapped nesting territories and assigned the closest large body of water as a pair's feeding grounds. This designation was

considered appropriate since eagles tend to nest near bodies of water from which they obtain food (Robertson 1978). Status (active, inactive) of eagle nests within the Kissimmee Basin was determined following guidelines prepared by Postupalsky (1974). The number of active and inactive territories was determined on a yearly basis from 1959–1979 for the Upper Basin, the Istokpoga Basin and the Lower Basin. Data were grouped as "during" construction (1962–1970) and "post" construction (1977–1979). Records before 1962 were omitted, and only data for the 1977–78 and 1978–79 seasons could be used for post-construction analyses because of the insufficient coverage of many territories before 1962 and between 1971 and 1977.

Reproductive success (number of young per active territory, number of young per successful territory) was calculated from "post" construction records only because the aerial surveys flown following construction were considered more accurate in approximating actual eagle production than the ground surveys conducted by Heinzman.

RESULTS AND DISCUSSION

The status and production of Bald Eagle territories in the Upper Basin, the Istokpoga Basin, and the Lower Basin during (1962–1971) and after (1977–1979) construction of the flood control project are summarized in Tables 1 and 2. The Upper Basin contained a higher average annual number of active territories both during and after construction than either the Istokpoga Basin or the Lower Basin (Table 2). However, the Lower Basin annually averaged 12 active territories per 1000 km^2 during construction as compared to 8.1 active territories per 1000 km^2 in the Upper Basin and

TABLE 1

STATUS AND PRODUCTION OF BALD EAGLES NESTING WITHIN THE KISSIMMEE BASIN, FLORIDA, 1962–1971, 1977–1979

Status or production	Sub-basins of the Kissimmee River Basin					
	Upper Basin		Istokpoga Basin		Lower Basin	
	D[a]	P[b]	D	P	D	P
Total active territories	201	63	20	10	132	12
Total inactive territories	27	20	10	2	23	1
Number of pairs that raised:						
0 young	29	18	5	3	19	2
1 young	48	17	8	2	29	7
2 young	25	16	3	4	12	1
3 young	—	2	—	—	—	—
Number active but results unknown	99	10	4	1	72	2
Total territories	327	93	34	13	227	15
Total young produced	98	55	14	10	53	9

[a] During construction (1962–1971).
[b] Post construction (1977–1979).

TABLE 2

BALD EAGLE NESTING STATUS SUMMARY FOR SUB-BASINS OF THE KISSIMMEE BASIN DURING AND AFTER CONSTRUCTION OF THE FLOOD CONTROL PROJECT

	Upper Basin		Istokpoga Basin		Lower Basin	
Number territories	D[a]	P[b]	D	P	D	P
Active/year	33.3	36.5	2.7	5.5	22.7	6.0
Inactive/year	3.0	10.0	1.1	1.0	2.6	0.5
Total	36.3	46.5	3.8	6.5	25.3	6.5

[a] D = During construction (1962–1971).
[b] P = Post construction (1977–1979).

1.6 active territories per 1000 km^2 in the Istokpoga Basin. Following channelization of the Kissimmee River, annual nesting activity in the Lower Basin declined to 3.2 active territories per 1000 km^2 vs 8.9 active territories per 1000 km^2 in the Upper Basin, and 3.2 active territories per 1000 km^2 in the Istokpoga Basin. Documented nesting activity (active territories per year) increased in both the Upper and the Istokpoga basins following construction, and decreased by 74% in the Lower Basin during this same period (Table 2).

Table 3 compares post-channelization production of nesting eagles in the three sub-basins to the production of eagles statewide and in the Central Region (Nesbitt et al. 1976) during the 1977 and 1978 nesting seasons. The productivity of eagles nesting in the Kissimmee Basin during these years was similar to that of eagles elsewhere in the state. These data indicate that the reproductive performance of the reduced number of ea-

TABLE 3

PRODUCTIVITY TOTALS FOR THE STUDY AREA, THE CENTRAL FLORIDA REGION[a], AND STATEWIDE[b], 1977–1978 THROUGH 1978–1979

Area	Active territories[c]	Successful nests	Young produced	Young/ successful nest	Young/ active territory
Upper Basin	52	34	55	1.57	1.06
Istokpoga Basin	9	6	10	1.67	1.11
Lower Basin	10	8	9	1.13	0.90
Central Florida	366	210	310	1.51	0.87
Statewide	672	405	586	1.45	0.87

[a] Boundaries of Central Florida region are delineated in Nesbitt et al. 1976.
[b] File data, Florida Game and Fresh Water Fish Commission.
[c] Totals include only those territories for which nest success was determined.

gles nesting in the Lower Basin has not been impaired since channelization of the Kissimmee River. In general, construction of the flood control project did not appear to have affected Bald Eagles nesting in the Upper and Istokpoga basins on a long-term basis. The observed increase in nesting activity following channelization almost surely was an artifact of more intensive aerial coverage of these areas. However, an actual increase in breeding birds could also explain this occurrence. It is possible that birds displaced from traditional nesting territories in the Lower Basin or elsewhere relocated in the Upper and Istokpoga basins. The Upper Basin in particular has consistently supported a large population of eagles and has recently been recommended for designation as "essential habitat" by the Southern Bald Eagle Recovery Team.

In the 1964–65 nesting season, Heinzman (unpubl.) noted at least 21 active, seven inactive and only one territory of unknown status in the Lower Basin in his field notes. We consider this figure of 21 active territories a valid minimum estimate of the pre-channelization nesting eagle population in the Lower Basin, since Heinzman (1965) reported that the number of breeding pairs remained practically constant between 1959 and 1965. In the early 1930's, Howell recorded the location of 13 active territories in the Kissimmee Basin (Howell and Heinzman 1967). All sites were still occupied in the 1962–63 season, and 12 were occupied in 1964–65. By contrast, only six active territories were observed during the 1978–79 breeding season in this same area during the annual aerial Bald Eagle nesting survey. The results of our investigation suggest that, since channelization, the Lower Basin no longer supports its historic density of breeding eagles.

Elimination of suitable nest trees in the Lower Basin was not observed by Heinzman and Heinzman (1970), and we do not believe a shortage of suitable nest-sites exists. Although a cause-and-effect relationship can not be demonstrated, two factors implicate construction of the flood control project and subsequent deterioration in forage availability in the Lower Basin as a probable major factor contributing to the decline in Bald Eagle nesting activity. The first is the occurrence of earliest recorded increases in nest desertions in the Lower Basin concurrent with construction of the flood control project (Heinzman and Heinzman 1970). Secondly, the decline in Bald Eagle nesting in the Lower Basin relative to other study area segments is consistent with the relative degree of ecosystem disruption resulting from project construction in the three study area segments. The impact of channelization on natural wetland ecosystems was most severe in the Lower Basin, where 78% (16,443 ha) of the marsh area was drained (Pruitt and Gatewood 1976). This drainage obviously had a devastating effect on productivity and marsh faunal associations (Milleson 1976, Pat-

rick 1978). Channelization of the Kissimmee River resulted in declines in sport fish populations (Montalbano et al. 1979a, 1979b), probable declines in total fish populations (Florida Game and Fresh Water Fish Commission 1957), probable declines in fish species diversity, and a 93% reduction in wintering duck and American Coot (*Fulica americana*) populations from pre-channelization levels (Montalbano et al. 1979a, 1979b). In addition to actually reducing the quantity of eagle prey sources, channelization has also made remaining forage comparatively less available to eagles. Prior to channelization, water levels characteristically peaked in October, then fell rapidly until the onset of the May rainy season (Montalbano et al. 1979b). This precipitous drop in water levels concentrated fish and waterfowl during the eagle nesting season. As water evaporated from depressions, dead and dying fish were available in great abundance to foraging eagles.

It follows that restoration of the pre-channelization ecosystem in the Lower Basin could possibly reestablish the prey base and could contribute to reversal of recent trends in Bald Eagle nesting activity.

SUMMARY

We analyzed the status of southern Bald Eagle (*Haliaeetus leucocephalus leucocephalus*) nesting during and after construction of a flood control project in the Kissimmee River Basin in central Florida. A 74% decrease in the annual number of active territories was observed following construction of this flood control project in that segment of the study area where disruption of aquatic ecosystems and, therefore, a prey base for eagles, was most severe. Productivity of eagles nesting in all three sub-basins was comparable to that of eagles nesting in central Florida and statewide between 1977 and 1979.

ACKNOWLEDGMENTS

We gratefully acknowledge the assistance provided by William B. Robertson, Jr., Stephen Nesbitt and Gerald Atmar in the critical review of this manuscript. David Scott provided copies of George Heinzman's eagle nesting records for the period 1959–1971.

LITERATURE CITED

Burns, L. 1976. Kissimmee River floodplain marsh model. Pp. III-1–III-102 *in* Water quality models for understanding potential eutrophication in Lake Okeechobee, Florida (H. T. Odum and F. G. Nordlie, eds.). Prepared for Florida Division of State Planning by the Center for Wetlands, Univ. Florida, Gainesville, Florida.

Dineen, J. W., R. L. Goodrick, D. W. Hallett and J. M. Milleson. 1974. The Kissimmee River revisited. Central and Southern Florida Flood Control District. In Depth Rept. Vol. 2. No. 2.

Florida Department of Administration. 1975. Interim report on the special project to prevent the eutrophication of Lake Okeechobee. Division of State Planning.

Florida Game and Fresh Water Fish Commission. 1957. Recommended program for Kissimmee River Basin. Florida Game and Fresh Water Fish Comm.

Goodrick, R. L. and J. F. Milleson. 1974. Studies of floodplain vegetation and water

level fluctuation in the Kissimmee River Valley. Central and Southern Florida Flood Control District. Tech. Publ. 74–2.

HEANEY, J. P., W. C. HUBER, P. B. BEDIENT, J. P. BOWDEN, S. GATEWOOD AND R. FULLER. 1975. Environmental resources management studies in the Kissimmee River Basin. Dept. Environ. Engin. Sci., Rept. ENV–05–75–1. Univ. Florida, Gainesville, Florida.

HEINZMAN, G. AND D. HEINZMAN. 1965. Kissimmee cooperative Bald Eagle sanctuary: a six year report. Florida Nat. 38:126–127.

——— AND ———. Kissimmee cooperative Bald Eagle sanctuary. Florida Nat. 43(4):175.

HOWELL, J. C. AND G. M. HEINZMAN. 1967. Comparison of nesting sites of Bald Eagles in central Florida from 1930 to 1965. Auk 84:602–603.

MILLESON, J. F. 1976. Environmental responses to marsh land reflooding in the Kissimmee River Basin. Central and Southern Florida Flood Control District, Tech. Publ. 76–3.

MONTALBANO, F., III, K. J. FOOTE, M. W. OLINDE AND L. S. PERRIN. 1979a. The Kissimmee River channelization: a preliminary evaluation of fish and wildlife mitigation measures. Pp. 508–515 *in* The mitigation symposium: a national workshop on mitigating losses of fish and wildlife habitats (G. A. Swanson, tech. coord.). Gen. Tech. Rept. RM–65, Rocky Mountain Forest and Range Exper. Stat.

———, ———, L. S. PERRIN AND M. W. OLINDE. 1979b. The Kissimmee basin wetlands investigation section: an interim report of studies. Florida Game and Fresh Water Fish Comm.

———, ———, M. W. OLINDE AND L. S. PERRIN. 1979c. Summary of selected fish and wildlife population data and assiciated recreational opportunities for the Kissimmee River Valley. Unpublished report. Florida Game and Fresh Water Fish Comm.

MURPHY, T. N., JR., AND J. W. COKER. 1978. The status of the Bald Eagle in South Carolina. Pp. 89–93 *in* Proc. Rare and Endangered Wildl. Symp. (R. R. Odum and L. L. Landers, eds.). Georgia Dept. Nat. Res. Tech. Bull. WL–4.

NESBITT, S. A., R. R. ROTH AND W. B. ROBERTSON. 1976. The status of the Bald Eagle in Florida 1972–1975. Proc. Southeastern Assoc. Game and Fish Comm. 29:424–428.

PATRICK, R. 1978. Some impacts of channelization on riverine systems. Pp. 15–28 *in* Environmental quality through wetlands utilization (M. A. Drew, ed.). Coord. Council Restoration of the Kissimmee River Valley and Taylor Creek-Nubbin Slough Basin.

POSTUPALSKY, S. 1974. Raptor reproductive success: some problems with methods, criteria, and terminology. Pp. 21–31 *in* Management of raptors (F. N. Hamerstrom, Jr., B. E. Harrell and R. R. Olendorff, eds.). Raptor Res. Rept. No. 2.

PRUITT, B. C. AND S. E. GATEWOOD. 1976. Kissimmee River floodplain vegetation and cattle carrying capacity before and after canalization. Florida Dept. Admin., Div. State Planning, Bur. Comp. Planning.

ROBERTSON, W. B., JR. 1978. Southern Bald Eagle. Pp. 27–30 *in* Rare and endangered biota of Florida, Vol. II, Birds (H. W. Kale, II, ed.). Univ. Presses of Florida, Gainsville, Florida.

SPRUNT, A., JR. 1954. Florida bird life. Coward-McCann, Inc., New York, New York and the National Audubon Society.

SPRUNT, A., IV, W. B. ROBERTSON, JR., S. POSTUPALSKY, R. J. HENSEL, C. E. KNODER AND F. J. LIGAS. 1973. Comparative productivity of six Bald Eagle populations. Trans. N. Am. Wildl. Conf. 38:96–106.

U.S. ARMY CORPS OF ENGINEERS. 1979. Kissimmee River, Florida reconnaissance report (Stage I). U.S. Army Corps of Engineers, Jacksonville District, Florida.

WEGENER, W. AND V. WILLIAMS. 1974. Extreme lake drawdown, a working fish management technique. Florida Game and Fresh Water Fish Comm.

——— AND ———. 1975. Fish population responses to improved lake habitat utilizing an extreme drawdown. Proc. Southeastern Assoc. Game and Fish Comm. 28:144–161.

KISSIMMEE BASIN WETLANDS INVESTIGATION SECTION, FLORIDA GAME AND FRESH WATER FISH COMMISSION, TAYLOR CREEK LODGE WEST, OKEECHOBEE, FLORIDA 33472. (PRESENT ADDRESSES: DIVISION OF WILDLIFE, FLORIDA GAME AND FRESH WATER FISH COMMISSION, 620 SOUTH MERIDIAN ST., TALLAHASSEE, FLORIDA 32301, WATERFOWL MANAGEMENT SECTION, FLORIDA GAME AND FRESH WATER FISH COMMISSION, TAYLOR CREEK LODGE WEST, OKEECHOBEE, FLORIDA 33472 AND FLORIDA AUDUBON SOCIETY, P.O. DRAWER 7, MAITLAND, FLORIDA 32751.) ACCEPTED 30 JUNE 1981.

Wilson Bull., 94(1), 1982, pp. 64–70

FUNGI AND RED-COCKADED WOODPECKER CAVITY TREES

Richard N. Conner and Brian A. Locke

It is widely thought that red heart fungus (*Phellinus pini* [Thore ex. Fr.]), syn. *Fomes pini*, must decay the heartwood of living pine trees (*Pinus* spp.) before Red-cockaded Woodpeckers (*Picoides borealis*) can excavate a cavity into the tree (Steirly 1957, Ligon 1971). Jackson (1977) reported that 20% of the red-cockaded cavity trees in the shortleaf (*P. echinata*) and loblolly (*P. taeda*) pines he sampled with an increment borer did not have visually detectable signs of red heart disease. He suspected, however, that the decay may have been in early stages or completely removed when the cavity was made.

P. pini has been the only fungus known to be found in red-cockaded cavity trees. Woodpeckers other than red-cockaded are dependent on trees with decayed heartwood, a condition that softens the heartwood and facilitates nest cavity excavation (Conner et al. 1976). In this instance, oaks (*Quercus* spp.) and hickories (*Carya* spp.) were the predominant tree species and the heart rot usually associated with them was *Spongipellis pachyodon* (Pers.) Kotl and Pouz.

The objectives of this study were to examine the internal conditions of red-cockaded cavity trees and determine presence or absence of decay, species of fungi involved and mode of entry of heartwood-decaying fungi into the trees.

METHODS

From 1977–1980, we examined 34 Red-cockaded Woodpecker cavity trees from the Angelina and Davy Crockett national forests and the I. D. Fairchild State Forest in east Texas. We searched these forests for recently killed cavity trees. Many trees had died from fire damage during prescribed burns (Conner and Locke 1979). Other causes of mortality were southern pine beetles (*Dendroctonus frontalis* Zimm.) and wind throw.

The trees we examined were either on the ground (N = 6) or standing (N = 28) in areas where many other cavity trees were present for red-cockadeds and their competitors. Since dead trees are typically not used by red-cockadeds for nesting or roosting (Ligon 1970), our impact on the woodpecker population was negligible.

Eighteen longleaf pines (*P. palustris*) (mean age = 108 years), 13 shortleaf pines (mean age = 90 years), and three loblolly pines (mean age = 90 years) were examined. Sections of trees with cavities or cavity starts were cut out, vertically sectioned and taken into the laboratory where chips of heartwood were aseptically extracted at 2–3 cm and 10–13 cm above and below cavities and cavity starts. The chips were cultured on malt agar at 25°C (see Conner et al. 1976 for technique). Heartwood from regions where decayed wood was adjacent to undecayed wood also cultured. Species of cultured fungi were determined by macroscopic and microscopic examination of the mycelial cultures (Davidson et al. 1942, Nobles 1965).

Presence or absence of decay prior to cavity excavation was estimated by careful visual examination of vertical sections of nest trees at each cavity site. *P. pini* grows in typical, thin, vertical columns of decay (2–10 mm in diameter). The older the infection within the tree, the more numerous the vertical columns and the larger their diameters. Often these columns are filled with thick masses of reddish-brown hyphal tissue. If a woodpecker excavated a cavity into a region of the tree where these decay columns were present in the heartwood, a vertical section of the cavity would show decay columns extending above and below the cavity. If decay occurred after the cavity was excavated, the cavity in effect would serve as a barrier and prevent spread of the decay. In the trees we examined, visual signs of decay at each cavity site were either totally lacking or present both above and below the excavated cavity.

RESULTS AND DISCUSSION

Heartwood decay was probably not an absolute prerequisite for Red-cockaded Woodpeckers to make a fully excavated cavity. Only 7 (39%) of the 18 longleaf pines examined were infected by heartwood decaying fungi; we detected no decay in 11 trees. Eleven (85%) of 13 shortleaf pines and all three loblolly pines examined had heartwood decay somewhere within the boles of the trees. If shortleaf and loblolly cavity trees are combined, 2 (12%) of these 16 trees did not have decayed heartwood. This is similar to the 20% figure observed by Jackson (1977) for the same tree species in Mississippi.

Presence of decay in the heartwood of a tree at one place in the bole did not necessarily mean that decay was present at all cavity sites within that tree. Examination of each cavity site revealed that 15 (47%) of 32 cavities in longleaf pines, 13 (87%) of 15 cavities in shortleaf pines, and 4 (100%) of 4 cavities in loblolly pines had decayed heartwood prior to cavity excavation (Table 1). Nineteen (37%) of the 51 cavities examined apparently were excavated into undecayed wood. Observations that Red-cockaded Woodpeckers can take a year or more to excavate a cavity (Baker 1971, Jackson 1977, Jackson et al. 1979) does not seem unreasonable in view of the firmness of healthy xylem tissue.

Four (31%) of 13 red-cockaded cavity starts were being excavated into longleaf pines with heart rots (Table 1); the remaining nine starts were being excavated into firm, undecayed wood. All three cavity starts in loblolly and shortleaf pines were being excavated into decayed heartwood.

A higher percentage of all cavities was excavated into decayed wood than were total cavity starts (Table 1). This suggests that some cavity starts that fail to hit decayed heartwood are aborted. However, this difference was not significant ($\chi^2 = 1.81$, $P > 0.26$) when tested with a 2×2 contingency table.

Although *P. pini* was the most common fungus (found in four longleaf, 10 shortleaf and two loblolly pines) *Phaeolus schweinitzii* (Fr.) Pat. (in one longleaf pine), *Lenzites saepiaria* (Wulf. ex. Fr.) Fr. (in one shortleaf pine),

Table 1
Occurrence of Heartwood Decay at Red-cockaded Cavities and Cavity Starts in East Texas Pine Trees

	Longleaf		Shortleaf		Loblolly		Total	
Cavity condition	N	%	N	%	N	%	N	%
Cavities								
Rot present	15	47	13	87	4	100	32	63
Rot absent	17	53	2	13	0	0	19	37
Cavity starts								
Rot present	4	31	1	100	2	100	7	44
Rot absent	9	69	0	0	0	0	9	56

Lentinus lepideus Fr. (in one loblolly pine), and *Phlebia radiata* Fr. (in one shortleaf pine) were also found in cavity trees. These four species of fungi were found in recently killed, standing cavity trees. *P. schweinitzii* is a common butt rot in pines that on occasion will spread several meters up the heartwood in the bole of a tree. The other fungi are thought to be dead wood and root decaying fungi (Overholts 1953). Obviously, decay of heartwood by these species can start before the tree is dead and has fallen. Two unidentified basidiomycetes were found in the heartwood of two longleaf pine cavity trees. One cavity tree contained two different species of fungi.

Researchers have suspected that Red-cockaded Woodpeckers introduce fungi (any species) as they begin to excavate a cavity and, as decay softens the sapwood, that the woodpeckers excavate the cavity entrance (Jackson 1977). Our results showed no indication of this sequence. As red-cockadeds excavated into sapwood tissue, pine gum (oleoresins) flowed to or was retained in the area of injury in apparently increased amounts, especially in longleaf pines. Pine gum had saturated the sapwood tissue surrounding the 67 cavity entrance tubes and cavity starts we examined. No fungus was ever detected in these saturated areas. Five cavity trees not included in our sample had lain on the ground for at least 3 years and had extensive decay in all other sapwood tissue except the areas around entrance tubes and starts that had been saturated with gum.

The heartwood of healthy, living pines is dead and thus does not saturate with oleoresins as does injured sapwood. Thus, woodpeckers may introduce *P. pini* or other basidiomycetes as they begin to excavate heartwood tissue in potential cavity trees (Jackson 1977). However, this was not apparent in our visual examinations of 32 cavities that had been vertically sectioned. At all the cavity sites where *P. pini* was present, columns of

decay were present in the heartwood throughout the entire cavity-site area prior to cavity excavation.

When *P. pini* grows within pines, it grows more rapidly vertically than horizontally due to the structure of the wood. Thus, a column of vertical decay (e.g., 25 cm) may include about 1 cm^2 of horizontal decay (pers. obs.). Compartmentalization of decay is a well-known phenomenon (Shigo and Marx 1977). A woodpecker's excavation through an existing pattern of decay columns can be detected with relative ease if the tree can be cut down and vertically sectioned.

We also examined the vertical sections of cavity trees to see whether Red-cockaded Woodpeckers had detected a small pocket of decay and subsequently excavated all of the decay in the shape of a cavity. If this occurred, it might appear that the birds had excavated a cavity in a tree without heartwood decay. Our observations on the growth pattern of *P. pini* within trees suggest this is not the case. In order for decay to have spread sufficiently to provide for the horizontal diameter of a cavity, it would have had to grow very extensively in both vertical directions, well beyond the vertical dimensions of a red-cockaded cavity.

When it was possible to determine the mode of entry of heartwood decay, the entry was through a broken branch stub. This supports Affeltranger's (1971) speculation that entry of decay in red-cockaded cavity trees was through branch stubs with exposed heartwood or through large wounds. Entry through large wounds would probably be less common; 10–12 cm of sapwood would have to be gouged out to expose the heartwood.

If basidiomycetes were present, they were usually found at both 2–3 cm and 10–13 cm below nest cavities. In many trees, we also cultured numerous species of imperfect fungi (species that do not reproduce sexually) and bacteria. When present, imperfect fungi and bacteria were always found in the zone closest to the bottom of the nest cavity. We doubt that Red-cockaded Woodpeckers rely on imperfect fungi to decay wood tissue and thus ease their task of cavity excavation. Imperfect fungi were more prevalent in older nest cavities and typically absent in freshly excavated ones. We suggest that imperfect fungi begin to infect the wood tissue on all surfaces of the inside of the cavity, but only after the cavity is complete. This is similar to what was observed in woodpecker nest cavities in hardwood trees (Conner et al. 1976) where a succession of different imperfect fungi and bacteria infected all the wood tissue around the completed nest cavities.

It is difficult for us to conclude how much Red-cockaded Woodpeckers depend on decay to soften the heartwood of living pines. The presence of heart rot prior to excavation was not required for all cavities. The rate of

occurrence of heart rot within cavity trees may just reflect the natural rate of occurrence of the fungi in the older trees within each forest community. Lay and Russell (1970) speculated that red heart is common in older stands and that woodpeckers could hardly avoid the fungus if they select older trees as cavity trees for reasons of tree size, wood density, or gum quality. Beckett (1971) also suspected that red heart was incidental to Red-cockaded Woodpecker selection of cavity trees.

We were not able to obtain current, accurate estimates of the frequency of heartwood decay in the longleaf stands and loblolly-shortleaf stands we examined. However, rough estimates of heartwood decay in loblolly and shortleaf pines in the Angelina and Davy Crockett national forests indicated a "moderate" infection rate (20–40%) for mature trees (G. E. Hartman, pers. comm.). Past estimates of the frequency of decay in Texas shortleaf pines, averaging 122 years of age, was 37% (Hepting and Chapman 1938). These frequencies are much lower than the frequency observed in our red-cockaded cavity trees (85%) in shortleaf pines. Frequency of decay in pine stands is variable and, in addition to age, is heavily dependent on stress factors such as excessive moisture and crowding (Wahlenberg 1946). Past frequencies of heartwood decay in other geographic areas were also lower than what we observed in shortleaf and loblolly pines: Arkansas loblolly—51% (mean age = 58 years), Arkansas shortleaf—11% (mean age = 120 years) (Mattoon 1915), Virginia Coastal Plain loblolly—19% (mean age = 110 years) (Nelson 1931), and North Carolina Coastal Plain loblolly—21% (mean age = 60 years) (Gruschow and Trousdell 1958). While this contrast tends to support the long held belief that Red-cockaded Woodpeckers prefer trees with decayed heartwood, it is still quite speculative because current frequencies of decay are needed to provide meaningful comparisons. Detection of heart rots by culture techniques is more efficient than simple visual examinations; thus, studies of decay frequencies from the past may have underestimated the actual presence of heart rots.

The frequency of decay in longleaf cavity trees was much lower than that in shortleaf or loblolly cavity trees (Table 1). Longleaf pines are well known for their copious production of gum, while shortleaf and loblolly pines produce much less (Wahlenberg 1946, Hodges et al. 1977). Because of the higher production of gum, longleaf pines have a higher resistance to invasion of fungi and bark beetles (Hodges et al. 1979). Gum can flow into injured tissue and slow or halt invasions. In fact, longleaf pine cavity trees have one-half the annual mortality rate of shortleaf and loblolly pine cavity trees (Lay 1973). Decay is not normally considered a problem in longleaf pines less than 100 years old (Wahlenberg 1946).

Mature stands of shortleaf and loblolly pines (70 years) would be ex-

pected to have a higher incidence of heart rot than similarly-aged stands of longleaf pines. Loblolly-shortleaf stands that are 70–80 years old should provide sufficient suitable cavity sites for Red-cockaded Woodpeckers. If red-cockadeds preferred longleaf pines with heart rot, a low frequency of suitably decayed longleaf pines may force some woodpeckers to use non-infected trees. Timber rotation ages (frequency of clearcutting) in longleaf pine forests (80 years in national forests) may not allow sufficient time for heart rot to develop to the extent and frequency necessary to be of most benefit to Red-cockaded Woodpeckers. It would require more time and energy to make cavities in nondecayed pines than in decayed pines. This may reduce the overall reproductive success of such birds and cause a gradual decline of populations in longleaf timber stands (see Conner 1979).

SUMMARY

Recently killed Red-cockaded Woodpecker (*Picoides borealis*) cavity trees were located during 1977–1980 in east Texas. Fungi from heartwood tissue at cavity sites and cavity starts was cultured on agar and identified. Heartwood decay was found in 63% of the cavity sites and 44% of the cavity-start sites examined. Longleaf pine cavity trees had a lower frequency of decay than did shortleaf and loblolly pine cavity trees. *Phellinus pini* was the most frequently detected fungus to be associated with red-cockaded cavity trees, but six other fungi species were detected. Our observations indicate that heartwood decaying fungi were not inoculated into the tree by the woodpeckers, but entered through broken branch stubs and were present prior to cavity excavation.

ACKNOWLEDGMENTS

We thank G. E. Hartman, Forest Wildlife Biologist, for his aid in obtaining cavity trees on the national forests in east Texas, D. J. Fox, District Forester, Texas Forest Service, for cooperation and assistance in obtaining cavity trees on the I. D. Fairchild State Forest, and F. F. Lombard, Center for Forest Mycology Research, Forest Products Lab, U.S.D.A. Forest Service, Madison, Wisconsin, for extensive aid and cooperation in checking our identifications of fungi cultures. We also thank J. A. Jackson, D. W. Lay, M. R. Lennartz and R. W. McFarlane for comments and constructive criticism of this paper.

LITERATURE CITED

Affeltranger, C. 1971. The red heart disease of southern pines. Pp. 96–99 *in* Symposium on the Red-cockaded Woodpecker (R. L. Thompson, ed.). Bur. Sport Fish. Wildl., USDI and Tall Timbers Res. Stat., Tallahassee, Florida.

Baker, W. W. 1971. Progress report on life history studies of the Red-cockaded Woodpecker at Tall Timbers Research Station. Pp. 44–49 *in* Symposium on the Red-cockaded Woodpecker (R. L. Thompson, ed.). Bur. Sport Fish. Wildl., USDI and Tall Timbers Res. Stat., Tallahassee, Florida.

Beckett, T. 1971. A summary of Red-cockaded Woodpecker observations in South Carolina. Pp. 87–95 *in* Symposium on the Red-cockaded Woodpecker (R. L. Thompson, ed.). Bur. Sport Fish. Wildl., USDI and Tall Timbers Res. Stat., Tallahassee, Florida.

Conner, R. N. 1979. Minimum standards and forest wildlife management. Wildl. Soc. Bull. 7:293–296.

———, O. K. Miller, Jr. and C. S. Adkisson. 1976. Woodpecker dependence on trees infected by fungal heart rots. Wilson Bull. 88:575–581.

——— and B. A. Locke. 1979. Effects of a prescribed burn on cavity trees of Red-cockaded Woodpeckers. Wildl. Soc. Bull. 7:291–293.

Davidson, R. W., W. A. Campbell and D. B. Vaughn. 1942. Fungi causing decay of living oaks in the eastern United States and their cultural identification. U.S. Dept. Agric. Tech. Bull. 785.

Gruschow, G. F. and K. B. Trousdell. 1958. Incidence of heart rot in mature loblolly pine in coastal North Carolina. J. For. 56:220–221.

Hepting, G. H., and A. D. Chapman. 1938. Losses from heart rot in two shortleaf and loblolly pine stands. J. For. 36:1193–1201.

Hodges, J. D., W. W. Elam and W. F. Watson. 1977. Physical properties of the oleoresin system of the four major southern pines. Can. J. For. Res. 7:520–525.

———, ———, ——— and T. E. Nebeker. 1979. Oleoresin characteristics and susceptibility of four southern pines to southern pine beetle (Coleoptera Scolytidae) attacks. Can. Entomol. 111:889–896.

Jackson, J. A. 1977. Red-cockaded Woodpeckers and pine red heart disease. Auk 94:160–163.

———, M. R. Lennartz and R. G. Hooper. 1979. Tree age and cavity initiation by Red-cockaded Woodpeckers. J. For. 77:102–103.

Lay, D. W. 1973. Red-cockaded Woodpecker study. Contrib. F. A. Proj. W–80–R–16 Job 10, Texas Parks Wildl. Dept., Austin, Texas.

——— and D. N. Russell. 1970. Notes on the Red-cockaded Woodpecker in Texas. Auk 87:781–786.

Ligon, J. D. 1970. Behavior and breeding biology of the Red-cockaded Woodpecker. Auk 87:255–278.

———. 1971. Some factors influencing numbers of the Red-cockaded Woodpecker. Pp. 30–43 *in* Symposium on the Red-cockaded Woodpecker (R. L. Thompson, ed.). Bur. Sport Fish. Wildl., USDI and Tall Timbers Res. Stat., Tallahassee, Florida.

Mattoon, W. R. 1915. Life history of shortleaf pine. Bull. U.S. Dept. Agric. No. 244.

Nelson, R. M. 1931. Decay in loblolly pine on the Atlantic Coastal Plain. Virginia For. Serv. Publ. 43:58–59.

Nobles, M. K. 1965. Identification of cultures of wood-inhabiting hymenomycetes. Can. J. Bot. 43:1097–1139.

Overholts, L. O. 1953. The polyoraceae of the United States, Alaska, and Canada. Univ. Michigan Press, Ann Arbor, Michigan.

Shigo, A. L. and H. G. Marx. 1977. Compartmentalization of decay in trees. U.S. Dept. Agric., For. Serv. Agric. Info. Bull. 405.

Steirly, C. C. 1957. Nesting ecology of the Red-cockaded Woodpecker in Virginia. Atlantic Nat. 12:280–292.

Wahlenberg, W. G. 1946. Longleaf pine: its use, ecology, regeneration, protection, growth, and management. Charles Lanthrop Pack For. Found., Washington, D.C.

WILDLIFE HABITAT AND SILVICULTURE LAB, SOUTHERN FOREST EXPERIMENT STATION, U.S. DEPT. AGRIC. FOR. SERV., NACOGDOCHES, TEXAS 75962 AND SCHOOL OF FORESTRY, STEPHEN F. AUSTIN STATE UNIV., NACOGDOCHES, TEXAS 75962. (PRESENT ADDRESS BAL: DEPT. BIOLOGY, NEW MEXICO STATE UNIV., LAS CRUCES, NEW MEXICO 88001.) ACEPTED 30 JUNE 1981.

Wilson Bull., 94(1), 1982, pp. 71–73

GENERAL NOTES

The humeroulnar pulley and its evolution in hummingbirds.—The humeroulnar pulley or trochlea humeroulnaris (*in* Nomina Anatomica Avium, J. J. Baumel et al., eds., Academic Press, London, England, 1979) is a ligament of the elbow in most birds (Fig. 1d). Originally named by Shufeldt (Myology of the Raven, McMillan and Co., London, England, 1890), the ligament extends from the caudal aspect of the medial epicondyle of the humerus to the ventral surface of the proximal end of the ulna. Buri (Jenaische Z. Naturwiss. 33:361–610, 1900) referred to the pulley (his "Ringband" and "Sehenschlinge") and noted some differences among different families. Sy (J. für Ornith. 84:199–296, 1936) illustrated the pulley but did not discuss its relation to M. flexor carpi ulnaris (FCU). More recently, the pulley has been mentioned in connection with its relationship to M. expansor secundariorum (Berger, J. Morph. 99:137–168, 1956), as well as in descriptive myology (Berger, Auk 85:594–616, 1968; Raikow, Auk 94:331–342, 1977). In none of these works has the pulley been thoroughly described and compared. The implication has been that, with few exceptions, this structure is essentially uniform. The purposes of this paper are to describe the structure and function of the pulley in its generalized state, to draw attention to its diversity, and to explain the unique pulley of hummingbirds (Trochilidae).

Our interest in the humeroulnar pulley grew out of our recent investigation of hummingbird myology. The pulley in hummingbirds is so unusual that we were compelled to look elsewhere to determine its homologies with a "normal" pulley. After dissecting representative forms from over 40 families, we determined the apparent ancestral condition for modern birds (Fig. 1b). Directional terms (dorsal, ventral and caudal) refer to the horizontally extended wing.

In most birds the pulley is best seen in ventral view. Its main structure can be likened to a loop, the cut ends of which have been spread sideways and attached to different bones (Fig. 1c). Ancestrally, it consists of three main parts that we call A, B and C (Fig. 1b). The main origin of the pulley, A or pars humeralis, is from the humerus. It arises from the caudolateral surface of the medial epicondyle of the humerus and passes superficial to the proximal portion of the tendon of M. flexor carpi ulnaris. It continues around and deep to that tendon (our part B or pars ulnaris) and inserts on the ventral surface of the ulna between the olecranon and the insertion of ligamentum collaterale ventrale. There is no demarcation between A and B in some birds; in others they are separated by an ossified or cartilaginous swelling of the pulley. A second humeral component, C or pars humeralis accessoria, arises from the ventral surface of the medial epicondyle of the humerus ventral and slightly distal to the origin of ligamentum collaterale ventrale. This component passes distally to join the main portion of the pulley between A and B. Pars humeralis (A) may be fused or unfused to the proximal end of the tendon of FCU. Pars humeralis accessoria (C) varies not only in size but in its proximity to A. Pars ulnaris (B) is the most constant feature, being present in all forms that have a pulley. We do not recommend use of the terms pars tendinea and pars pennata as introduced and described for the Rock Dove (*Columba livia*) in J. J. Baumel et al. (1979:152) because we regard pars tendinea as a synonym of trochlea humeroulnaris, and pars pennata to be a largely tendinous portion of M. expansor secundariorum.

The primary function of the pulley is to keep the belly of FCU in constant relation to the ulna. That is, in extreme flexion of the forearm the pulley prohibits the tendon and belly of FCU from moving proximally along the humerus. It (especially C) also helps to bind the elbow against separation at its medial surface. The pulley may also function as a point of origin for one of three parts of M. expansor secundariorum (ES). Humeral and scapular origins of ES are not considered here and all further references to that muscle refer to the

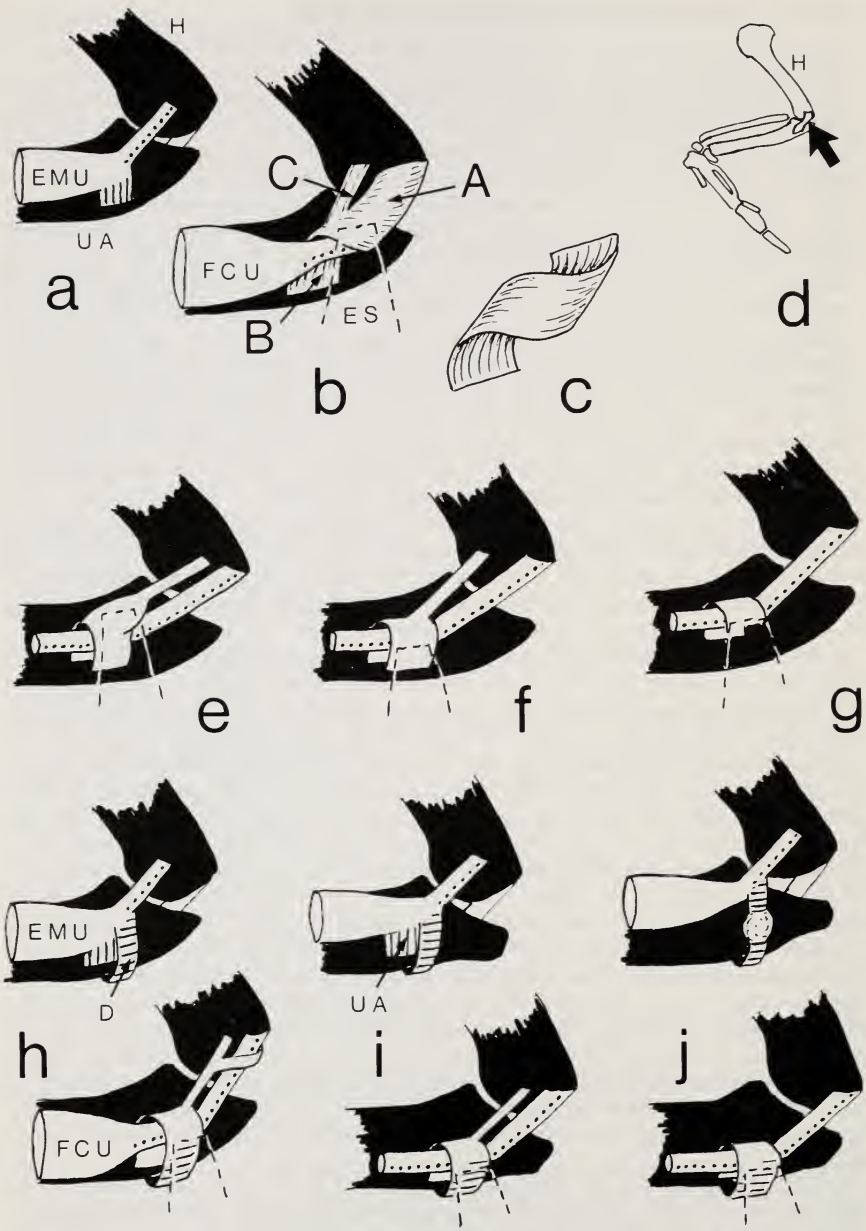


FIG. 1. Diagrams of the humeroulnar pulley and its associated structures: a. dorsal view of elbow. b. ventral view of elbow showing generalized form of pulley: A = pars humeralis; B = pars ulnaris; C = pars humeralis accessoria. c. diagram of parts A and B to show main structure of pulley. d. right wing, ventral view, showing location of pulley. e, f, g. ventral

portion from the humeroulnar pulley (Fig. 1b). In a few orders ES contributes to the stabilization of FCU, but primitively it arises directly from the pulley and has no relation to that muscle.

An essentially primitive form of the pulley is characteristic of the Sulidae, Ardeidae, Anatidae, Rallidae, Charadriidae, Falconiformes, Galliformes, and the majority of land birds from pigeons (Columbidae) to the passerines (Passeriformes). The typical oscine pulley is very reminiscent of the ancestral form described above with one important exception. The tendinous origin of ES from the pulley has shifted somewhat caudally and distally and, in combination with B, has acquired the additional function of guiding the tendon of FCU. The need for A is correspondingly reduced, and A is weak in some passerines. Reduction or loss of C may also occur. Loss of one or both of the humeral components of the pulley (A and C) appears to have occurred independently in unrelated groups. In most suboscines A is reduced to a slender band that crosses the tendon of FCU and C is present but noticeably reduced (Fig. 1h). In the swifts (Apodidae) only C is present (Fig. 1i), and in the crested-swifts A is present, but C is lost. In the Tinamidae only B is present (Fig. 1g). It serves as a point of origin for ES which, together with B, forms a hook that restrains the tendon of FCU. Columbidae lack C and ES is ligamentous. In the Procellariidae (Fig. 1f) and Laridae (Fig. 1e) B forms a loop on the ulna and C is present; ES plays no role in restraining the tendon of FCU. In at least one family (Spheniscidae), FCU is represented only by a tendon and the pulley is absent.

In hummingbirds both A and C are lost (Fig. 1j); only the attachment to the ulna (B) remains. In addition, a ligamentous sling (D) containing a large sesamoid arises from the tendon of origin of M. extensor metacarpi ulnaris, passes around the caudal border of the ulna, and fuses with what remains of the pulley. The tendon of FCU passes through the loop formed by this sling and the pulley (B). ES arises from the pulley and also serves to guide the tendon of FCU. Other differences between the ancestral condition and that of hummingbirds become more meaningful when the ulnar anchor is understood and morphological intermediates are examined (Fig. 1h, i, j).

The ulnar anchor, a short tendinous slip, arises from the tendon of origin of M. extensor metacarpi ulnaris, a large muscle on the dorsal side of the forearm in most birds. The anchor passes caudally and inserts on the caudodorsal surface of the ulna (Fig. 1a, h, i). Investigation of the myology of hummingbirds alone might lead one to conclude that the ligamentous sling (D) represents a modified ulnar anchor. However, in suboscines and swifts, both a ligamentous sling and an ulnar anchor are present (Fig. 1h, i). Hummingbirds lack the ulnar anchor. Thus, the humeroulnar pulley of hummingbirds probably evolved from the primitive condition by loss of A and C and the ulnar anchor, and elaboration of a new structure, D, found elsewhere only in swifts and suboscines.

This paper represents a cursory survey of variation in the humeroulnar pulley, based on only a single species from most of the families examined. In view of its structural diversity we recommend that a detailed description of the humeroulnar pulley be included in future works on the wing muscles of birds.—Gregory Dean Bentz and Richard L. Zusi, *National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.* (Present address GDB: *Mount Vernon College, Washington, D.C. 20007.*) *Accepted 1 Dec. 1980.*

←

views showing pulleys of Laridae, Procellariidae and Tinamidae, respectively. h, i, j. dorsal views (above) and ventral views (below) of a suboscine, Apodidae and Trochilidae, respectively. D = tendinous sling; EMU = M. extensor metacarpi ulnaris; ES = M. expansor secundariorum; FCU = M. flexor carpi ulnaris; H = humerus. Bones are black; muscle tendons shaded with dots; ulnar anchor vertically hatched; tendinous sling (D) horizontally hatched; M. expansor secundariorum shown as if transparent by dashed outline.

Wilson Bull., 94(1), 1982, pp. 74–79

Relationships of environmental factors to onset of autumn morning vocalizations in an Ozark community.—Birds frequently vocalize near daybreak but little quantitative work exists concerning environmental factors which may affect the precise onset of vocalizations (Armstrong, A Study of Bird Song, Oxford Univ. Press, London, England, 1963). However, a few detailed studies deal with the relationship of song activity to time of day and light (e.g., Wright, Auk 29:307–327, 1912; Wright, Auk 30:512–537, 1913; Allard, Am. Nat. 64:436–469, 1930; Emlen, Bird-Banding 8:81, 1937; Groebbels, Ornithologische Mitteilungen 8:61–66, 1956; Leopold and Eynon, Condor 63:269–293, 1961). Our objective was to quantitatively assess the relationships of several environmental factors to time of first vocalization in bird communities in the forested Ozarks during autumn. If the microclimate is physically ideal for sound transmission at dawn (Henwood and Fabrick, Am. Nat. 114:260–274, 1979), it may be reasonable to associate many communicative auroral bird sounds with climatic factors. Therefore, we include all bird vocalizations (song, call, chip, scold, etc.) in our analysis.

Study region.—The study was conducted in the White Rock Wildlife Management Area/ Ozark National Forest, in northwestern Arkansas. This region includes several hundred square km of unbroken upland oak-hickory forest in the 25–50 year class with occasional farm clearings and abandoned fields containing grasses and shrubs. The topography is hilly with 150 m local relief rising to 670 m above mean sea level.

Methods.—Five secluded areas were visited in random order from 30 min before dawn until 30 min after sunrise, between late August and December 1978, until each area was studied an average of five mornings. Relative humidity (percent, using a sling psychrometer), wind speed (km/h, using a Dwyer wind meter, held 1.5 m above ground) and barometric pressure (inches of mercury, barometer) were measured at the start and conclusion of each visit. Ambient air temperature (°C), light intensity (foot-candles, photometer facing open sky in clearings), percent cloud cover (visual estimate) and local time (CST) were recorded as each bird species was first heard vocalizing.

Multiple linear and stepwise correlation and regression (step-up model) analyses were performed between the time of first vocalization (Y) per morning per species and eight independent variables—time of sunrise (Sun), elevation (Elev), relative humidity (Hum) (arcsine-transformed), ambient temperature (Temp), light intensity (Lite), wind speed (Wind), percent cloud cover (ClCov) (arcsine-transformed) and barometric pressure (BaroP). This was done for each of 11 species with 10 or more morning records (N = 178 bird-mornings). Data on six species with more than four but fewer than 10 morning records were analyzed by univariate analyses only (totalling 35 bird-mornings).

Results.—Time of first vocalization, recorded 232 times for 28 species, was positively correlated with time of sunrise, wind speed, cloud cover and barometric pressure most often (Table 1). However, time of sunrise and light intensity together accounted for over 92% of the variance in vocalization time in stepwise correlation and regression (77 and 15%, respectively; $P < 0.001$; other independent variables seldom explained a statistically significant fraction of variance; Table 2). The large component of the variance accounted for by time of sunrise alone means that it can serve as a useful predictor of time of first vocalization (Table 3).

For birds with 10 or more records, we performed partial correlation analysis with the effects of time of sunrise held constant to better understand the association of other variables to time of first vocalization (Kerlinger and Pedhazur 1973; Table 1). This analysis shows that light intensity and percent cloud cover were associated with time of first vocalization for many species. Too few data were obtained for 11 species to warrant analysis.

Table 1

Simple (and Partial)[a] Correlations Between Environmental Variables and Time of First Vocaliztion for Birds with Five or More Morning Records

Species	Number of mornings	Environmental variables[b]							
		Sun	Elev	Hum	Temp	Lite	Wind	ClCov	BaroP
Cardinalis cardinalis (Cardinal)	19	0.96***[c]				(0.94)***	0.79***	(0.66)**	0.76***
Carduelis tristis (American Goldfinch)	13	0.96***				(0.86)***	0.75**	0.61* (0.88)***	0.84***
Melanerpes carolinus (Red-bellied Woodpecker)	14	0.93***				(0.86)***	0.65*	0.60*	
Colaptes auratus (Common Flicker)	18	0.93***				(0.73)**	0.71***	0.66** (0.66)**	0.62**
Corvus brachyrhynchos (Common Crow)	23	0.95***		(0.68)**		0.62** (0.89)***	0.71***	(0.57)*	0.60**
Cyanocitta cristata (Blue Jay)	15	0.65**			(0.61)*	(0.80)**	0.51*		
Dryocopus pileatus (Pileated Woodpecker)	16	0.90***					0.73***		0.65*
Dumetella carolinensis (Catbird)	10	0.94***			−0.77**				
Parus carolinensis (Carolina Chickadee)	5	0.88*		0.95*					

Table 1
Continued

Species	Number of mornings	Environmental variables[b]							
		Sun	Elev	Hum	Temp	Lite	Wind	ClCov	Baro P
Picoides pubescens (Downy Woodpecker)	11	0.92***				(0.91)***		0.63*	0.67*
Pipilo erythrophthalmus (Rufous-sided Towhee)	18	0.97***			−0.48*	0.66** (0.76)**	0.76***		0.73***
Sitta carolinensis (White-breasted Nuthatch)	21	0.93***		(0.66)**		(0.99)***	0.75***		0.49*
Thryothorus ludovicianus (Carolina Wren)	6	0.91*		0.94**					
Turdus migratorius (American Robin)	5	0.98**							
Vireo griseus (White-eyed Vireo)	6								−0.97*
Wilsonia citrina (Hooded Warbler)	6	0.95**					0.91*		
Zonotrichia albicollis (White-throated Sparrow)	7	0.78*							

[a] Partial correlation with variable time of sunrise held constant for birds with 10 or more records is in parentheses.
[b] Sun = time of sunrise (CST); Elev = elevation (m); Hum = relative humidity (%); Temp = ambient temperature (°C); Lite = light intensity (foot-candles); Wind = wind speed km/h); ClCov = % cloud cover; BaroP = barometric pressure (inches of mercury). Hum and ClCov values were arcsine-transformed.
[c] Significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; blank space $P > 0.05$.

TABLE 2

PERCENTAGE VARIANCE (R^2) ACCOUNTED FOR BY SIGNIFICANT ($P < 0.05$, F-STATISTICS) ENVIRONMENTAL VARIABLES AND MULTIPLE STEPWISE REGRESSION EQUATIONS FOR TIME OF FIRST VOCALIZATION FOR BIRDS WITH 10 OR MORE MORNING RECORDS

Species	Minimum no. of records	Significant environmental variables (% variance)[a]	Stepwise regression equation
C. cardinalis	16	$X_1(92)$, X_2 = Lite(7)	$Y = -0.46 + 1.012X_1 + 0.161X_2$
C. tristis	12	$X_1(92)$, X_2 = ClCov(6)	$Y = -0.13 + 0.983X_1 + 0.004X_2$
M. carolinus	14	$X_1(87)$, X_2 = Lite(10)	$Y = -1.76 + 1.243X_1 + 0.022X_2$
C. auratus	17	$X_1(87)$, X_2 = Lite(7), X_3 = ClCov(3)	$Y = -0.23 + 1.002X_1 + 0.015X_2 + 0.003X_3$
C. brachyrhynchos	19	$X_1(90)$, X_2 = Lite(8), X_3 = ClCov(1)	$Y = -0.20 + 0.971X_1 + 0.054X_2 + 0.001X_3$
C. cristata	13	$X_1(42)$, X_2 = Lite(37), X_3 = ClCov(15)	$Y = -0.43 + 1.004X_1 + 0.013X_2 + 0.004X_3$
D. pileatus	16	$X_1(82)$	Same as Table 3
D. carolinensis	10	$X_1(89)$	Same as Table 3
P. pubescens	11	$X_1(85)$, X_2 = Lite(13)	$Y = -1.36 + 1.173X_1 + 0.031X_2$
P. erythrophthalmus	14	$X_1(95)$, X_2 = Lite(3), X_3 = Hum(1)	$Y = -2.31 + 1.205X_1 + 0.210X_2 + 0.008X_3$
S. carolinensis	17	$X_1(86)$, X_2 = Lite(14)	$Y = -1.63 + 1.224X_1 + 0.018X_2$

[a] X_1 = time of sunrise (CST) = Sun; Lite = light intensity (foot-candles); ClCov = % cloud cover (arcsine-transformed); Hum = relative humidity (arcsine-transformed); Y = time of first vocalization (CST).

Table 3

Mean Deviations and Regression Equations Between Time of Sunrise and Time of First Vocalization for Birds with Five or More Morning Records

Species	Equation[a]	Mean deviation[b]
C. cardinalis	Y = −0.30 + 1.00X	−19.4
C. tristis	Y = −0.71 + 1.11X	−1.7
M. carolinus	Y = −2.14 + 1.33X	+0.3
C. auratus	Y = −1.15 + 1.18X	+2.0
C. brachyrhynchos	Y = −1.07 + 1.13X	−16.0
C. cristata	Y = 1.27 + 0.79X	−2.0
D. pileatus	Y = −0.44 + 1.08X	+5.1
D. carolinensis	Y = −0.01 + 0.94X	−23.0
P. carolinensis	Y = −1.92 + 1.29X	+3.5
P. pubescens	Y = −0.88 + 1.14X	+1.5
P. erythrophthalmus	Y = −2.37 + 1.31X	−25.8
S. carolinensis	Y = −1.56 + 1.24X	−3.6
T. migratorius	Y = −1.70 + 1.24X	−5.2
T. ludovicianus	Y = −0.22 + 1.07X	−15.0
V. griseus	Y = 4.24 + 0.29X	+4.1
W. citrina	Y = −2.09 + 1.36X	+5.2
Z. albicollis	Y = 1.05 + 0.81X	−17.5

[a] Y = time of first vocalization (CST), X = time of sunrise.
[b] Mean min before (−) or after (+) time of sunrise (CST) for first vocalization.

Discussion.—Closely related species usually respond similarly to similar environmental factors. In this study, birds in the same family (Picidae) usually first vocalized within 5 min of each other (Table 3, unpubl.).

We have studied several ecological factors common to all avian species of a given community. We might expect all avian species of a community to display temporal cohesiveness in behavior towards these factors since factors which affect one species in the community could have similar effects on other avian species of the same community. That is, many of the same environmental obstacles to genic survival are confronted by all avian species of a given community. Thus we might expect optimal adaptations for a particular set of ecological conditions regardless of the degree of genetic relatedness. For example, in our study all but one cavity nester (3 tits, 5 woodpeckers) first vocalized on average ±5 min within time of sunrise (N = 87 bird-mornings) (Table 3, unpubl.). Birds that lived in the earlier stages of succession (*C. cardinalis*, *D. carolinensis*, *P. erythrophthalmus* and Brown Thrasher [*Toxostoma rufum*]) all vocalized about 20 min before sunrise (N = 49 bird-mornings), earlier than all studied species (Table 3, unpubl.). Furthermore, nearly all the environmental factors we studied were similarly associated to time of first vocalization in each species (Tables 1, 2 and 3).

We have established correlations between several environmental factors and the timing of a behavioral trait. Since different species confronted with similar environmental factors have independently evolved similar timing of this trait, in effect we have found supportive evidence for the hypothesis that these environmental factors are responsible for the course of evolution that time of first vocalization has taken (*sensu* Alcock, Animal Behavior: an Evolutionary Approach, Sinauer, Sunderland, Massachusetts, 1979:204).

Alternatively, the correlations may be a result of one species vocalizing as soon as it hears another species vocalizing. In our study, vocalizations were not arranged in any specific order with respect to species but this hypothesis needs further study.

At any rate, our data support the possibility that similar proximal factors mold the epigenetic systems of birds of a given community causing congruence and convergence in many behaviors. This could form a coevolved complex of behaviors, behaviors which were associated with each other and with the environment.

Julie Zammuto helped in the field and typed rough drafts. F. L. Ramsey provided statistical advice. C. R. Preston and G. Moore assisted with computer analysis and F. Burnside provided stimulating discussion. R. W. Knapton, J. S. Millar and E. H. Miller provided comments on earlier drafts.—Richard M. Zammuto and Douglas James, *Dept. Zoology, Univ. Arkansas, Fayetteville, Arkansas 72701.* (Present address RMZ: *Kananaskis Centre for Environmental Research, Univ. Calgary, Seebe, Alberta T0L 1X0 Canada.*) *Accepted 20 Feb. 1981.*

Wilson Bull., 94(1), 1982, pp. 79–81

Possible courtship behavior by Snowy Owls in winter.—Sutton (Mem. Carnegie Mus. 12:3–267, 1932), Watson (Ibis 99:419–462, 1957), Taylor (Living Bird 12:137–154, 1973) and others have described the breeding behavior of Snowy Owls (*Nyctea scandiaca*). Courtship consists of vocalizations, and ground and aerial displays used principally by males. Behavior resembling some elements of these displays has been reported on the wintering grounds. Mitchell (Can. Field-Nat. 61:68–69, 1947) described an owl with white plumage (male?) and another with very heavy markings (female?), that were seen perched together in a field in mid-March. The birds took flight at dusk, rose to a considerable height, and flew northwards side by side. Weir (Ont. Field Biol. 27:3–17, 1973) observed a small white owl (male) and a larger, darkly-barred owl (female) standing on the ground 1 m apart, swaying and bobbing their heads at each other, on 5 March. These actions were occasionally interrupted by short, joint flights, and the birds remained together for at least 5 h. Such reports may have led to the claim that Snowy Owls may arrive on the breeding grounds already mated (e.g., Karalus and Eckert, The Owls of North America, Doubleday, New York, New York, 1973). Except for these two brief observations, the nature and frequency of courtship outside the breeding season is unknown. This note describes several cases of possible courtship observed during a study of this species near Calgary, Alberta, and suggests the significance of such behavior.

Observations were made with 20–40× telescopes and recorded on a cassette recorder. The owls were observed at a distance of 50–200 m from a parked automobile. Sexes were identified by plumage characteristics and size (Witherby et al., The Handbook of British Birds, Vol. 2, H. F. and G. Witherby, London, England, 1938; Portenko, Die Schnee-Eule, Neue Brehm-Bucherei, No. 454, A. Ziemsen Verlag, Wittenberg, 1972; Josephson, J. Field Ornith. 51:149–160, 1980). Adult males are almost immaculately white. Adult females were distinguished from immature males by their larger size and by the absence of the mottled coverts characteristic of immature birds. The heavy barring and conspicuously mottled coverts of immature females permit their recognition. We have verified the validity of these plumage characters on over 50 specimens whose sex and age were confirmed by internal dissection and molt pattern (Lein, unpubl.).

Observations.—On 9 February 1978, an adult male was perched on an 8 m high utility pole, hooting at a female on a similar perch 400 m away. The male had been observed in the area for 2 days, and the female had been resident since mid-January. From 16:26–16:30, the

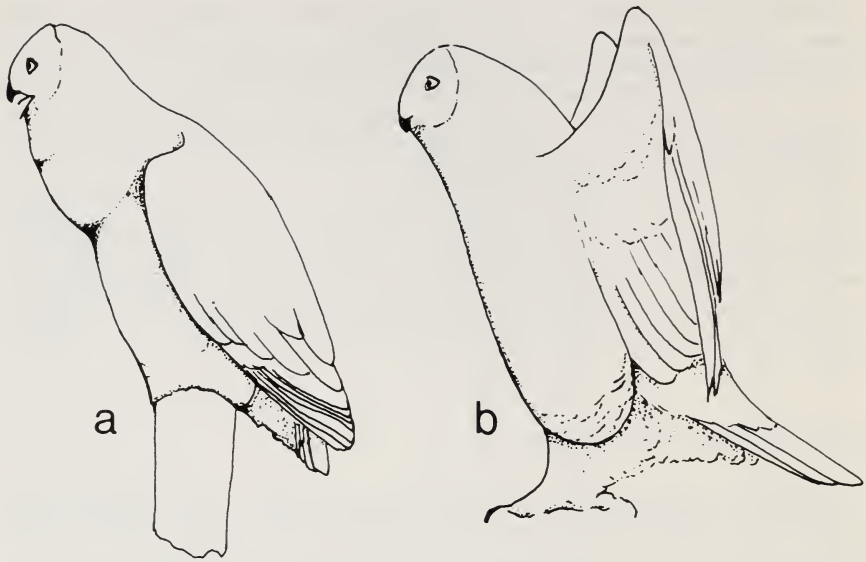


FIG. 1. Postures of male Snowy Owls during possible courtship activity: (a) hooting posture; (b) "ground display." Drawings made from photographs and field sketches.

male gave low volume hoots while facing the female. Each hoot consisted of two notes, resembling *whoo-whoo*; calls were separated by a 10–15-sec interval. The male's tail was held below the plane of the body and his wings were not extended (Fig. 1a). There was no observable reaction by the female. At 16:31 the male flew out of sight, away from the female, and was not seen in the area again.

On 25 February 1978, an adult male and two females were observed from 14:00–16:45. (Neither female was the bird involved in the previous observation; both were territorial residents.) The male was perched on a 25 m high steel powerline tower. One female (A) was on a similar perch 800 m from the male and the other (B) was perched 1600 m from the male on a 12 m high utility pole. From 14:00–14:51 the male watched both birds. At 14:52 the male hooted very softly. The posture and calls were identical to those described above. The bird hooted until 15:00, turning its head towards female A between calls. Shortly afterward, female A flew away, and the male's hooting was interrupted by a bout of preening. At 16:05 he flew about 400 m and landed on another powerline tower, still about 1600 m from female B. The flight did not resemble the undulating courtship flight described by Taylor (1973, fig. 7), but the wing-beats were more pronounced than in normal flight. After perching the male actively preened, looked around and shifted on the perch. Following several hooting calls at 16:41, he performed a display (Fig. 1b) that resembled Taylor's (1973, fig. 9) "ground display" in body posture and wing position. Males on the breeding grounds typically perform this courtship display with a lemming in their possession; we were unable to see whether the male we observed had a prey item in his feet. He continued hooting while displaying and slowly turned 90° to face the female, then turned back to face his original direction. After about 15 sec he flew directly toward the female. The male was lost from sight, but the female remained on the perch. There was no indication of aggressive behavior between these birds.

Discussion.—Some Snowy Owls are territorial in winter (Keith, Can. Field-Nat. 78:17–24, 1964; Boxall, M.Sc. thesis, Univ. Calgary, Calgary, Alberta, 1980), and one might suggest that the behavior patterns described in our observations represent territorial behavior. However, several lines of evidence argue against this explanation. First, in 5 years of study we have observed that males wintering in the Calgary region rarely defend territories but that many females do (Boxall 1980). Most males that we observed stayed in an area for only 1 or 2 days and then disappeared. Evans (Am. Birds 34:748–749, 1980) has noted a similar sexual difference in territorial behavior.

Second, in our observations the males appeared to be directing vocal and visual displays specifically toward females. The distances between the males and females in our observations may seem extreme for courtship interactions, but breeding males have been observed to display to females over 500 m away (Taylor 1973).

Third, in 29 obvious territorial interactions between wintering Snowy Owls we did not observe behavior patterns similar to those described in this note. Four of these interactions were between males and females.

We did not note vocalizations by owls during territorial interactions although Evans (1980) has. Snowy Owls have been described as relatively silent on the winter range (e.g., Witherby et al. 1938), and hooting by males has previously been reported only on the breeding grounds (e.g., Sutton 1932, Taylor 1973). Such hooting is very loud, being audible at distances of 2 miles (3.2 km) (Sutton 1932). Taylor (1973) mentions two forms of hooting: territorial hooting or song, in which the male lifted its tail while vocalizing, and quieter threat hooting, in which the bird maintained an upright posture and did not lift its tail. The hooting we describe was not loud (barely audible 400 m away), and the bird was upright with its tail lowered (Fig. 1a).

The posture of the male in the second observation (Fig. 1b) is very similar to that of males presenting prey while courting females (Taylor 1973), although we could not ascertain whether our male had a prey item. Also, we recorded the male hooting while displaying, whereas Taylor described males as being silent during such displays.

We suggest that our observations were of incipient courtship behavior. We observed no reactions by females to the males and therefore, the behavior may be non-functional. However, there is some evidence that some Snowy Owls may move north in pairs. We have observed a male and a female perched together (within 10 m) on over a dozen occasions in late February or March. This type of close association was not seen earlier in the winter. One of us (PCB), Weir (1973) and G. A. Webber (pers. comm.) have observed pairs of owls flying north at high altitudes in March, and Fyfe (Blue Jay 17:114, 1959) described a concentration of pairs of owls in Saskatchewan from 30 March–1 April 1959.

These observations suggest that some owls may arrive on the arctic breeding grounds already mated. The breeding cycle of Snowy Owls is quite long relative to the short arctic summer (Parmelee, Beaver 303:30–41, 1972). Therefore, pairing during late winter may allow owls to compress their breeding cycle, and to increase reproductive success allowing more time to raise young from large clutches of 11–13 eggs (Watson 1957). Only more detailed studies of the owls on their winter range, and of owls arriving on the breeding grounds, can confirm this hypothesis.

We thank W. F. Parsons for assistance in the field, and Charles Mamo for drawing the figure. M. L. Chamberlin and R. J. Clarke provided valuable comments on the manuscript. Our research was supported by grants from the Canadian Wildlife Service, the University of Calgary, and the Natural Sciences and Engineering Research Council of Canada.—Peter C. Boxall and M. Ross Lein, *Dept. Biology, Univ. Calgary, Calgary, Alberta T2N 1N4 Canada. (Send reprint requests to MRL.)* *Accepted 30 Mar. 1981.*

Wilson Bull., 94(1), 1982, pp. 82–83

Differential hunting success in a group of Short-eared Owls.—Differential hunting success between adults and immatures has been documented for a number of avian species, e.g., Adelie Penguin (*Pygoscelis adeliae*) (Ainley and Schlatter, Auk 89:559–566, 1972); Brown Pelican (*Pelicanus occidentalis*) (Orians, Anim. Behav. 17:316–319, 1969); Olivaceous Cormorant (*Phalacrocorax olivaceous*) (Morrison et al., Wilson Bull. 90:414–422, 1978); Little Blue Heron (*Florida caerulea*) (Recher and Recher, Anim. Behav. 17:320–322, 1969); and Sandwich Tern (*Sterna sandvicensis*) (Dunn, Ibis 114:360–366, 1972). All of the above species are single-brooded, lay small clutches, have relatively long periods of post-fledging parental care (in the form of direct feeding), and exhibit delayed reproduction. Ashmole and Tovar (Auk 85:90–100, 1968) hypothesized a relationship between the length of time required by young birds to attain hunting skills equal to adults and certain life-history characteristics; young individuals of species with the life-history characteristics listed above were predicted to attain hunting skills equal to adults over a relatively long period of time. Conversely, young individuals of species with opposite life-history characteristics were predicted to attain hunting skills equal to adults over a short period of time. This study documents an example that may differ from the prediction of Ashmole and Tovar (1968).

The Short-eared Owl (*Asio flammeus*) occurs over most of continental North America and is known to shift locally and regionally, presumably in response to the abundance of its major food, voles (*Microtus* spp.) (Clark, Wildl. Monogr., No. 47, 1975). *A. flammeus*, in contrast to the species listed above, lays relatively large clutches, apparently is multiple-brooded in middle latitudes (Lockie, Bird Study 2:53–69, 1955), and has a short period of post-fledging parental care (in the form of direct feeding) (Clark 1975), but exhibits considerable flexibility with regard to time and locale of breeding and clutch-size. Thus, based on the hypothesis of Ashmole and Tovar (1968), young individuals of *A. flammeus* are predicted to have attained hunting skills equal to adults.

During a period from 24 January to 30 January 1976, we observed a group of *A. flammeus* consisting of three individuals: one individual was completely white underneath, leading us to believe that this individual was an adult male (Bent, Life Histories of North American Birds of Prey, Pt. 2, Dover Publications, Inc., New York, New York, 1961; Chapman, Handbook of Birds of Eastern North America, Dover Publications, Inc., New York, New York, 1966; Clark 1975), another individual was light-buffy underneath, leading us to conclude that this individual was an adult female (Bent 1961, Chapman 1966), the remaining individual was uniformly dark-buffy underneath, and on two occasions we observed it beg for food from a distance of 1–2 m (the adult bird ignored it). From these observations we concluded that this individual was an immature bird. This group may have been a family group; however, we have been unable to find any literature concerning post-breeding family cohesiveness in owls.

The group generally arrived in the area 1 h before sunset. The area was a snow-covered (ca. 250 mm in depth) oldfield habitat in Meridian Twp., Ingham Co., Michigan. Individuals either perched on a fence post for a short period of time or began coursing the area in search of voles; if a strike was successful the individual usually flew a distance of approximately 100 m and devoured the vole. Table 1 summarizes the results of the hunting successes of the members of the group.

Contingency tables were used to compare the success rates of (1) the adult male vs the adult female, and (2) the adults combined vs the immature. The success rates of the adult male vs the adult female were not significantly different ($\chi^2_c = 1.456$, df = 1, $P > 0.1$). The combined success rates of the adults vs the immature were significantly different ($\chi^2_c =$

Table 1
Hunting Success of a Group of Short-eared Owls

Date	Adult male		Adult female		Immature	
	Success	Failure	Success	Failure	Success	Failure
24 January 76	5	1	0	0	1	6
27 January 76	2	0	1	0	0	3
28 January 76	0	1	3	4	0	0
29 January 76	1	0	0	1	0	0
30 January 76	4	3	3	4	1	2
Totals	12	5	7	9	2	11

5.099, df = 1, $P < 0.01$). This analysis, though the sample size is small, shows the young *A. flammeus* had not attained hunting skills equal to the two adults.

We conclude that the hypothesis of Ashmole and Tovar (1968) may be contradicted, and disparate life-history characteristics may be related to the lengthy attainment of adult hunting skills. The species first mentioned (all fish-eaters) apparently have a stable food resource and can reliably support themselves and a small brood over a long period of time, whereas the owl must track an unpredictable food resource, breeding only when a rich food resource is found. After breeding, when food supplies may decline in an area, adult *A. flammeus* appear to lead their young (if this group was a family group), intentionally or otherwise, to resource-rich areas, which may constitute an indirect form of post-fledging parental care that is adaptive by increasing the probability of young attaining enough food to survive. If the group we studied was not a family group, then perhaps young follow adults to resource-rich areas. Such a behavior implies that effective resource-tracking may have a learning basis in "nomadic-type" birds.

Acknowledgments.—We thank D. L. Beaver, L. Harper, R. J. Raitt, and three anonymous reviewers for comments on the manuscript.—Thomas G. Marr and Douglas W. McWhirter, *Dept. Zoology, Michigan State Univ., East Lansing, Michigan 48823.* (Present address TGM: *Dept. Ecology and Evolutionary Biology, Univ. Arizona, Tucson, Arizona 85721.*) *Accepted 20 Feb. 1981.*

Wilson Bull., 94(1), 1982, pp. 83–84

Observations at a Laughing Falcon nest.—Little is known of the breeding biology of the Laughing Falcon (*Herpetotheres cachinnans*), a species occurring from Mexico to southern Argentina. Several nests of this species have been found (Wolfe, Condor 56:161–162, 1954; Skutch, Animal Kingdom 63:115–119, 1960; Haverschmidt, Birds of Surinam, Oliver and Boyd, London, England, 1968; Mader, pers. comm.), but little has been published on activities at the nests.

On 15 July 1979, we located a nest containing a single nestling in the crotch of a tree (*Bombax* sp.) along the Río Limón, east of Hacienda Boca Chica, 22 km north of Olmos, Dpto. Lambayeque, Perú (5°30′S, 79°43′W), at 400 m. Both slopes of the valley were covered with dry, deciduous forest. The nest was in a crotch formed by three large limbs radiating

upward from the main trunk about 12 m above the ground. Two epiphytic cacti on the north side of the nest provided protection from the mid-day sun. No nest material was apparent, coinciding with observations of others (Brown and Amadon, Eagles, Hawks and Falcons of the World, McGraw-Hill, New York, New York, 1968; Wolfe 1954).

Evidently the nestling was several weeks old as judged by its size (nearly as large as the adult), its ability to feed itself, and the amount of whitewash at the nest-site. The nestling closely resembled the adult in plumage, but the rectus was yellower than the adult's. During the period of observation (11:20–16:36) the adult(s) brought three snakes to the nestling.

The first snake, originally 45 cm long, was delivered (less the anterior 8 cm previously eaten by the adult) at about 11:28. The nestling received an intact snake of the same size at 15:31. At 15:40 an adult arrived at the nest with a larger snake, similar in appearance but lacking its head.

The usual nest-site of this falcon is in a tree cavity, although it has previously nested in the crotches of trees (Haverschmidt 1968, Brown and Amadon 1968). In the apparent absence of cavities it has used old nests of other raptors in southwestern Ecuador (Grossman and Hamlet, Birds of Prey of the World, C. N. Potter, New York, New York, 1964). In the locality where we observed the nest, large trees that could potentially provide cavities were scarce. This may explain why the above nest was in a crotch of a *Bombax*.

On the west slope of the Peruvian Andes the Laughing Falcon was previously recorded only from Lechugal, Dpto. Tumbes, ca. 210 km north of our observation (Hellmayr and Conover, Catalogue of Birds of the Americas 13:242, Field Museum, Chicago, Illinois, 1949). J. William Eley and Thomas S. Schulenberg (pers. comm.), however, saw this species in late October 1977 on the Río Quiróz, southwest of Ayabaca, Dpto. Piura, suggesting that this falcon may be local but widespread in the little-known canyons of northwestern Perú.

We thank J. V. Remsen, Jr., J. P. O'Neill, M. D. Williams and T. S. Schulenberg for comments on the manuscript. We are most grateful to John S. McIlhenny, H. Irving and Laura R. Schweppe, and Babette M. Odom for their support of our fieldwork. Antonio Brock E., Marc Dourojeanni R., Susana Moller H., and Carlos Ponce P. of the Dirección General Forestal y de Fauna, Lima, Perú, continue their support and issued the necessary permits. We acknowledge the continued collaboration of Aero Perú.—Mark B. Robbins and David A. Wiedenfeld, *Museum of Zoology, Louisiana State Univ., Baton Rouge, Louisiana 70893.* *Accepted 9 Dec. 1980.*

Wilson Bull., 94(1), 1982, pp. 84–85

Evidence of Bald Eagles feeding on freshwater mussels.—A 1978 study of the winter habitat of the Bald Eagle (*Haliaeetus leucocephalus*) in the Coconino National Forest, Arizona, indicated repeated and potentially heavy use of a freshwater mussel (*Anodonta corpulenta*) in the eagles' diet. As many as 10 eagles (five adults and five immatures) were observed at Upper Lake Mary near Flagstaff when the junior author collected field data between 27 February and 10 March. However, only 2–3 eagles were present in the area through most of the winter. No foraging activity was seen, but a variety of circumstantial evidence was collected, suggesting more than casual use of this mussel.

Innumerable shell fragments and pieces of mussel tissue, as well as 4–5 broken shells and three intact shells with the contents removed, were scattered on the snow beneath favored eagle perch trees along the shoreline. Pieces of shell also were found in five of seven identifiable eagle castings. In the shoreline mud, where mussels were trapped and exposed after a rapid lowering of the water level, eagle tracks were abundant; however, no sign of other birds or mammals was observed there or in the snow beneath the perches. In Texas, win-

tering Bald Eagles have been reported feeding on freshwater clams under similar conditions of receding lake waters (Nielson, p. 93 *in* Wintering of the Migrant Bald Eagle in the Lower 48 States, Spencer, ed., Natl. Agric. Chem. Assoc., Washington, D.C., 1976).

Invertebrates are mentioned infrequently in Bald Eagle food habits literature and then only as insignificant prey items. The only other recorded observation of a freshwater bivalve serving as eagle food came from Dunstan and Harper's (J. Wildl. Manage. 39:140–143, 1975) study of prey remains at six eagle nests in Minnesota, where invertebrates (one clam [*Lampsilis* sp.] and one crayfish [*Cambarus* sp.]) accounted for 2% of the items collected. In western Washington, less than 2% of the food of nesting Bald Eagles was made up of crustaceans (Retfalvi, Condor 72:358–361, 1970). Most other reports are from Alaska, where an analysis of 435 eagle stomachs showed an average of less than 2% invertebrates (33 crabs [*Cancer magister*], one octopus, one shrimp and one amphipod) (Imler and Kalmbach, USDI Fish & Wildl. Serv., Circ. 30, 1955); on Kodiak Island three invertebrates (two blue mussels [*Mytilus* sp.] and one shrimp) were recorded in 114 food items (Grubb and Hensel, Murrelet 59:70–72, 1978); and on Amchitka Island less than 1% of the prey was found to be invertebrate (four octopi and one amphipod) (Sherrod et al., Living Bird 15:143–183, 1977). In 1936, in the Aleutian Islands, Murie (Condor 42:198–202, 1940) noted an apparently unusual 16% invertebrate composition (one squid, six snails, four crabs and one Nereid), but in 1937 no invertebrates were recorded.

This *Anodonta* was probably introduced from the Mississippi Valley in the 1930's or 1940's, through the glochidial stage on the gills of yellow perch (*Perca flavescens*) or northern pike (*Esox lucius*). We can only speculate from the abundance of broken shells below perches that the eagles used their hooked beaks and strong, sharp talons to break the molluscs apart, rather than dropping them onto rocks from the air as reported for other less well equipped scavengers such as gulls (*Larus* sp.) and crows (*Corvus* sp.) (Siegfried, S. Afr. J. Sci. 73:337–341, 1977; Zach, Behaviour 68:106—117, 1978). However, Golden Eagles (*Aquila chrysaetos*) have been documented using the aerial technique to break turtle shells (Fisher et al., Beitr. Vogelkd. 21:275–287, 1975).

Wintering Bald Eagles are opportunistic feeders, normally consuming fish, birds and mammals as available. Although data were insufficient for quantification, it appears that mussels comprised a notable portion of the eagles' diet at Upper Lake Mary during the study period. Other food items included waterfowl (American Coot [*Fulica americana*]), channel catfish (*Ictalurus punctatus*), northern pike, rainbow trout (*Salmo gairdneri*) and several unidentified mammals. It is unlikely that freshwater mussels are consistently a major prey item; however, they represent an alternate food source that may be heavily used when abundant and/or readily accessible.

The authors wish to thank D. Prigge, IV, for field assistance; D. Bancroft and J. Landry for helpful information on the mussels and fisheries of Upper Lake Mary; and T. Dunstan, H. Hudak, R. Knight, D. Spencer and R. Szaro for reviewing the manuscript. Funding was provided by the U.S.D.A. Forest Service, Southwestern Region, through the coordination of C. Kennedy.—Teryl G. Grubb, *Rocky Mountain Forest and Range Experiment Station, Forestry Sciences Lab., Arizona State Univ., Tempe, Arizona 85287* and Michael A. Coffey, *Resource Management, Sequoia-Kings Canyon National Park, Three Rivers, California 93271.* *Accepted 20 Feb. 1981.*

Wilson Bull., 94(1), 1982, pp. 85–87

Killdeers feeding on frogs.—On 13 July 1980 we observed several Killdeers (*Charadrius vociferus*) feeding on small anurans in an experimental fish pond near Starkville, Oktibbeha

FIG. 1. An adult Killdeer with *Hyla cinerea*.

Co., Mississippi. The approximately 10 m by 20 m pond was normally 1 m deep, but had been drained, leaving puddles of water over approximately 20% of its bottom. The bottom was free of vegetation. Schardien drove to the edge of the pond at 11:05. Two grown young and one adult Killdeers were present. Between 11:05 and 11:10 one of the young birds ate three anurans, one of which was positively identified as a green tree frog (*Hyla cinerea*). At 11:21 this same Killdeer ate another frog and two more Killdeers landed in the drained pond. Schardien remained at the pond until 11:39, during which time four more frogs were captured and eaten by an adult (Fig. 1) and two volant juveniles.

When Schardien and Jackson returned to the pond at 12:04, eight Killdeers were present. Between 12:04 and 12:36 at least 11 more anurans—some definitely *H. cinerea*—were captured. One unidentified anuran was captured and discarded. In between frog catching sorties, the Killdeers stood quietly, watching the grassy north perimeter of the pond where most of the frogs were captured. At times the Killdeers displayed and charged at one another. When a Killdeer sighted a frog, it rushed towards it, grasped it with its mandibles, and shook it. The frog appeared to die almost immediately. The Killdeers rushed from distances as great as 5 m to capture frogs; most attempts were successful. When a Killdeer rushed towards a frog, the other Killdeers were instantly alert and one or more of them would also rush to the scene. Once a frog was captured, attempts were often made to steal it. Twice frogs were eaten by a bird other than the one who caught it. Once a Killdeer knocked a frog from the bill of another bird and ate it. Two Killdeers were observed rinsing a frog before eating it and we observed several Killdeers running to the puddles as if intending to wash a frog, but eating it when pursued by other Killdeers. In at least two of these cases the bird drank after eating a frog.

We returned to the pond at 18:00 and found six Killdeers present; one continuously "pa-

trolled" the pond perimeter as if searching for frogs. One frog was caught during an hour of observation.

The food habits of Killdeers have been well studied in many parts of the country (e.g., New York: Eaton, Memoir 12, New York State Museum, Albany, New York, 1910:351; Nebraska: Aughey, First Rept., U.S. Entomol. Comm., App. 2, 1878:49; U.S.: McAtee and Beal, U.S.D.A. Farmer's Bull. No. 497 (revised) 1924:14–16). Food washing has been previously reported (Bunni, The Killdeer, *Charadrius v. vociferus* Linnaeus, in the breeding season: ecology, behavior, and the development of homoiothermism. Ph.D. dissertation, Univ. Michigan, Ann Arbor, Michigan, 1959:174), but to our knowledge the only previous report of Killdeers eating vertebrate prey is that of Weston (Auk 80:550–551, 1963) who saw a Killdeer eat dead minnows. A review of the literature for other charadriids suggests that the Black-bellied Plover (*Pluvialis squatarola*), the American Golden Plover (*P. dominica*), and the Snowy Plover (*Charadrius alexandrinus*), in rare circumstances will take vertebrates. These records included small fish (both *Pluvialis* species: Palmer, pp. 153–159 *in* The Shorebirds of North America, Stout, ed., Viking Press, New York, New York, 1967; Sprunt and Chamberlain, South Carolina Bird Life, Univ. South Carolina Press, Columbia, South Carolina, 1970), lizards (*P. dominica*) (Palmer 1967), and small frogs (*C. alexandrinus* in Egypt) (Latham, A General Synopsis of Birds, Vol. III, Leigh & Sotheby, London, England 1785:204). The involvement of several Killdeers and the frequency with which they ate frogs could have been related to the concentration of frogs along the edge of the drying pond and to the extremely hot, dry weather in the area which may have reduced arthropod food resources during the previous month.—Bette J. Schardien and Jerome A. Jackson, *Dept. Biological Sciences, Box GY, Mississippi State Univ., Mississippi State, Mississippi 39762.* *Accepted 22 Dec. 1980.*

Wilson Bull., 94(1), 1982, pp. 87–89

Possible use of legs as dissipators of heat in flying Cliff Swallows.—Several authors have shown that unfeathered portions of the legs of passerine birds can function as dissipators of heat (Steen and Steen, Acta Physiol. Scand. 63:285–291, 1965; Tucker, J. Exper. Biol. 48:67–87, 1968; Murrish, Comp. Biochem. Physiol. 34:859–869, 1970; Frost and Siegfried, Zool. Afric. 10:101–108, 1975) but quantified description of leg extending behavior in a large number of wild passerines over a range of temperatures appears to be lacking.

The purpose of this paper is to document the range of temperatures at which wild Cliff Swallows (*Petrochelidon pyrrhonota*) extend their legs, probably to dissipate heat.

Methods.—I observed up to 138 post-breeding Cliff Swallows sunning on the roof of the Creston Valley Wildlife Interpretation Centre, approximately 10 km west of Creston, British Columbia, on warm, sunny days between 21 July and 7 August 1980. During the period I recorded the air temperature in direct sunlight using a thermometer held 1 m above ground level approximately 7–10 m from the swallows. The air temperature on the roof was recorded on only four occasions because it disrupted the swallows' sunning activity. I counted the number of Cliff Swallows that left the roof following a bout of sunning with their legs extended and retracted. I also recorded the proportion of Cliff Swallows with legs extended after sunning that panted upon perching in willows (*Salix* sp.).

Results and discussion.—When the air temperature and roof temperature exceeded approximately 21°C and 29°C, respectively, approximately 50% of the Cliff Swallows extended their legs (Fig. 1). Nearly all the swallows extended their legs at an air temperature of 28°C (roof temperature 38°C) (Fig. 1). The reasons why the Cliff Swallows extended their legs are unclear. Perhaps the swallows were simply cooling their feet. However, that Cliff Swallows

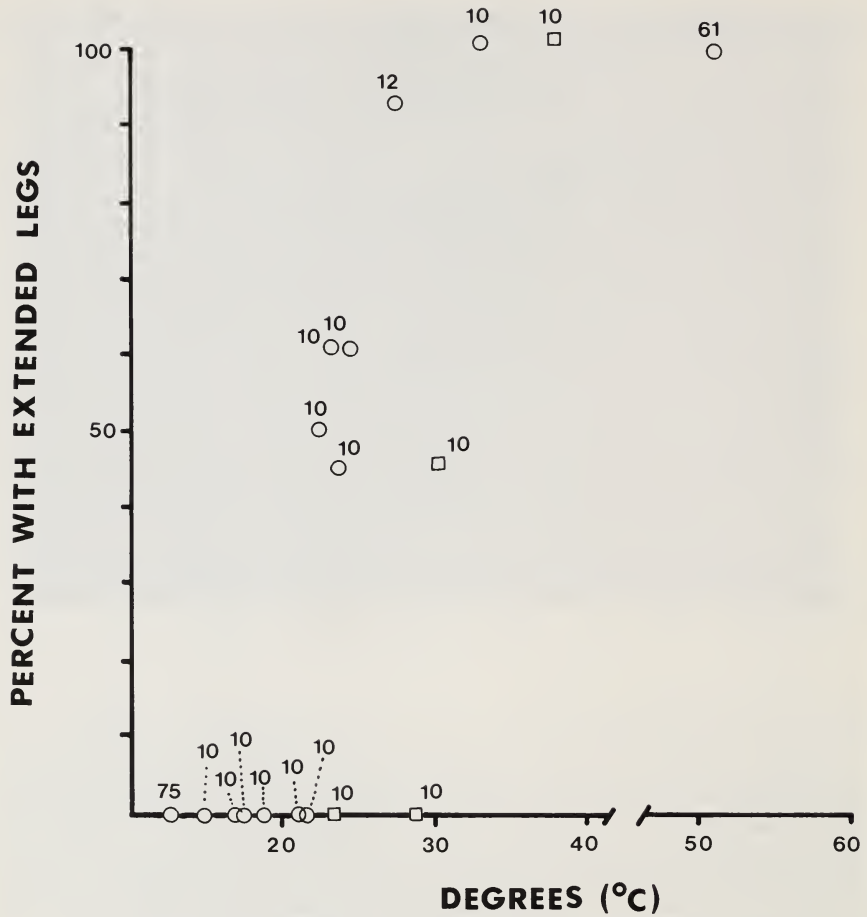


FIG. 1. Percentage of Cliff Swallows that extended their legs and temperature. Sample sizes are indicated opposite each data point. ○ = air temperature, □ = roof temperature.

used their legs to dissipate heat following sunning is suggested by several facts. On 21 July, when the roof temperature was 51.7°C, 60 of 61 Cliff Swallows that left the roof following a bout of sunning extended their legs, whereas only one of eleven swallows returning to the roof to begin sunning had its legs extended. In addition, 20 of the swallows that extended their legs alighted in a willow and all of those swallows panted. It is well known that birds pant to dissipate heat (Welty, The Life of Birds, W.B. Saunders, Philadelphia, Pennsylvania, 1975:130). Only two swallows were seen leaving the roof with their legs retracted and neither of them panted. On occasion individual Cliff Swallows appeared to drag their extended legs in ponds and sloughs, possibly to increase heat dissipation. This was quite different from the skimming behavior of Cliff Swallows that drank while flying. Drinking swallows lowered the head, opened the bill and appeared to scoop water into the mouth which left a V-shaped

ripple on the water surface whereas leg-dipping swallows appeared to plop their legs and perhaps tail in and out of the water in a quick motion.

Frost and Siegfried (1975) found that two species of swallow (*Hirundo cucullata* and *H. albigularis*) in South Africa extended their legs in 90–100% of the cases at a mean ambient temperature of 38°C. Those results compare closely with mine for the Cliff Swallow. However, unlike my findings, the same authors found no leg extension response in either species at mean temperatures of 27°C or 33°C. Possibly South African swallows are adapted to breed in warmer climates than the Cliff Swallow population at Creston and, therefore, have a higher tolerance to high temperatures.

I thank D. Flook, A. Gaunt, S. Lustick, K. Vermeer and an anonymous referee for commenting on the manuscript.—ROBERT W. BUTLER, *Canadian Wildlife Service, P.O. Box 340, Delta, British Columbia V4K 3Y3, Canada.* *Accepted 7 Feb. 1981.*

Wilson Bull., 94(1), 1982, pp. 89–90

Active anting by the Yellow-shouldered Blackbird.—Many temperate species (Potter, Auk 87:692–713, 1970), including Red-winged Blackbirds (*Agelaius phoeniceus*), display anting behavior (Nero, Auk 68:108, 1951). Other than records for the Puerto Rican Tanager (*Nesospingus speculiferus*) (King and Kepler, Auk 87:376–378, 1970), there are no reported cases of anting by West Indian birds. Reports of this behavior in the widespread genus *Agelaius* are rare. For these reasons, the following observations of active anting by the Yellow-shouldered Blackbird (*A. xanthomus*) are of interest. An actively anting individual applies ants to its body, as opposed to merely allowing ants to invade the body surface.

We saw Yellow-shouldered Blackbirds ant once on 6 March 1974, at 08:20 (1 h 33 min after sunrise) near La Parguera, Puerto Rico. A group, varying from 15–20 birds, gathered on bare ground at the edge of a scrubby pasture. The birds were within 10–15 cm of each other. At least 19 different Yellow-shouldered Blackbirds actively anted during the 8-min period that the flock continued this activity. Also in the flock were three Shiny Cowbirds (*Molothrus bonariensis*) and a Greater Antillean Grackle (*Quiscalus niger*), none of which actively anted. The anting behavior resembled that described for other passerines (Simmons, Zool. Soc. London 149:145–162, 1966). The Yellow-shouldered Blackbirds applied the ants mainly to the remiges, but also to the rectrices, breasts and upper tail coverts. Their tails were often under the body while the birds anted their remiges, the tips possibly in contact with the tails. Five times individuals fell on their sides while applying ants to their wings. Whitaker (Wilson Bull. 69:195–262, 1957) noted such tumbling by an anting Orchard Oriole (*Icterus spurius*). The plumages of the anting yellow-shoulders were fluffed and wings were drooped, while the remiges were spread.

Ant density at the site was about 100 per 0.1 m^2, and we could only find the workers of a harvest ant (*Pheidole* sp., Myrmicinae). The night before it had rained 23 mm, the first heavy rain in several months. Potter (1970) suggested a relationship between rainfall and anting. She also pointed out that anting is most likely during periods of molt, but in this instance it is doubtful if any of the blackbirds were molting, as most, if not all, of the birds were adults, and the Yellow-shouldered Blackbird's postnuptial molt takes place during August–December. There is no prenuptial molt in adults.

Anting could reduce infestation by Mallophaga and Acarina. In 1974–1975 at La Parguera, 69% of 265 blackbirds had Mallophaga (Post, J. Field Ornith. 52:16–22, 1981). The chemical constituents of ants which are of value to anting birds vary between ant subfamilies. Harvest ants do not secrete formic acid, as do members of Formicinae, which are commonly used by anting birds (Simmons 1966). Myrmicinae are usually avoided because of their stings. How-

ever, these ants do secrete anal fluids that are potentially insecticidal.—William Post, *Box 582, Aiken, South Carolina 29801* and Micou M. Browne, *Dept. Entomology, North Carolina State Univ., Raleigh, North Carolina 27607.* *Accepted 5 Mar. 1981.*

Wilson Bull., 94(1), 1982, pp. 90–93

Competition between Red-winged Blackbirds and Common Grackles.—Interspecific competition is often difficult to document in natural situations because species pairs or groups are commonly studied after they have long been in contact (see for example, Cody, Competition and the Structure of Bird Communities, Princeton Univ. Press, Princeton, New Jersey, 1974). It is therefore difficult to know what effect each species had on the reproductive success of the other at the time of initial contact when competition was presumably most intense. Although Red-winged Blackbirds (*Agelaius phoeniceus*) and Common Grackles (*Quiscalus quiscula*) have long been sympatric, they frequently do not nest in the same habitat. Despite the fact that cattail marshes may have been an original nesting habitat for grackles (Stepney, Ph.D. thesis, Univ. Toronto, Toronto, Ontario, 1979), they are generally considered now to be prime nesting habitat for red-wings and, in many areas, rather unusual nesting substrate for grackles (Wiens, Auk 82:356–374, 1965). Occasionally, however, grackles do nest in such areas. The present study documents a possible effect of the arrival of grackles on red-wing reproductive success in a cattail marsh. For a comparison of red-wing and grackle nesting behavior, as well as for a description of the interaction between the two species, see Wiens (1965).

In 1974 the senior author studied red-wings on four marshes (Redwing Slough, Crawdad Slough, 87th Street Slough and Long John Slough) located in Palos Park Forest Preserve about 45 km outside Chicago, Illinois. In 1978 both authors worked on two of the four marshes (Redwing Slough and the south end of 87th St. Slough). In 1974 no grackles nested on any of the four marshes. In 1978 grackles nested on Redwing Slough although none nested on the other three marshes. The present study compares reproductive success of red-wings nesting on Redwing Slough before and after the arrival of grackles. In addition, reproductive success of red-wings on this marsh in 1978 is compared with that on 87th St. Slough where no grackles nested.

The two marshes emphasized in this study were located 1.5 km apart. Both Redwing Slough and the southern end of 87th St. Slough contained six red-wing territories each year. The principal emergent vegetation on the marshes was cattails (*Typha* spp.). Redwing Slough also contained substantial amounts of buttonbush (*Cephalanthus occidentalis*). A detailed description of the marshes and the methods used in making various measurements is presented in Lenington (Anim. Behav. 28:347–361, 1980). Harem sizes were estimated by determining the minimum number of females required to account for the number of nests on a territory (Holm, Ecology 54:356–365, 1973). Because females renest readily if a nest is destroyed, there were usually more nests on a territory than there were females.

In both marshes in 1974 and 1978 I measured the size of each male's territory, the density of cattails on the territory and the number of females nesting on the territory. In addition, in 1978 I noted the date on which females settled on territories. Nests were checked every 2–5 days to determine fledging success.

In 1978, four pairs of grackles nested on Redwing Slough. The grackles occupied small nest-centered territories within the area of the larger red-wing territories. Grackles nested exclusively within the cattail portion of the marsh; none nested in buttonbush. It is possible that grackles selected Redwing Slough for nesting while not nesting on the other three marshes because Redwing Slough appeared to be the highest quality marsh (when studied

Table 1
Comparison of Redwing and 87th St. Sloughs in 1974 and 1978

	Redwing 1974	Redwing 1978	87th St. 1974	87th St. 1978
Mean cattail density of territories (stems/m^2)	5.45 (0.78)[a]	10.49 (0.96)	6.51 (1.17)	11.73 (0.94)
Mean territory size (m^2)	660 (123.67)	578.3 (105.09)	1139 (58.9)	1676 (73.26)
Date of arrival of first female	2 April	11 April	7 April	4 April
Date when all territories had at least one female	—	27 April	—	11 April
Mean harem size	7.17 (1.17)	3.50 (0.43)	2.00 (0.32)	2.33 (0.33)
Date of first nest	2 May	7 May	4 May	7 May
Mean clutch-size	3.56 (0.07) [52][b]	3.70 (0.15) [23]	3.41 (0.11) [22]	3.42 (0.15) [17]
Proportion of successful nests	0.685 [54]	0.483 [29]	0.115 [26]	0.222 [18]
Mean no. of young fledged from successful nests	2.00 (0.18) [37]	3.00 (0.28) [14]	1.67 (0.33) [3]	2.25 (0.25) [4]

[a] Value in parentheses is standard error of the mean.
[b] Value in brackets is sample size where not given in text.

in 1974 it had the largest harems, highest proportion of nests fledging young and largest number of young fledged from successful nests of any of the four marshes).

Grackles tended to nest earlier than red-wings. Three grackle nests were started in the week of 25 April–1 May and one was started the following week. In contrast, only one red-wing nest had been started by 8 May and the peak of red-wing breeding did not occur until the week of 23–29 May.

A comparison of the characteristics of red-wing territories and the components of red-wing reproductive success in 1974 and 1978 is presented in Table 1. The major change in red-wing reproductive success potentially attributable to grackles is a reduction in harem size. Mean harem size on Redwing Slough was significantly smaller in 1978 than in 1974 ($t = 2.96$, df = 10, $P < 0.02$), whereas mean harem size on the 87th St. Slough was unchanged between the two years ($t = 0.69$, df = 10, $P > 0.05$). In addition, as can be seen by the data on the date all territories had at least one female, females settled considerably later on Redwing Slough than they did on 87th St. Slough. A cursory examination of other nearby marshes that did not contain grackles showed that they also had large numbers of females at a time when few females were found nesting on Redwing Slough. In contrast, the first female seen on any of the four marshes studied in 1974 was on Redwing Slough.

As discussed in Lenington (1980), red-wing harem size within (although not between) marshes near Chicago is positively correlated with cattail density and territory size. However,

TABLE 2
COMPARISON OF MEAN AND VARIANCE OF RED-WING HAREM SIZES FROM 14 LOCALITIES

Location	No. of years studied	Mean (unweighted)	Between-year variance	Reference
Mann and Beaver lakes	2	2.91	0.058	Orians (1980)
30 Acre and Little McDowell lakes	2	2.84	0.031	Orians (1980)
TNWS	2	2.85	0.045	Orians (1980)
CNWS	4	5.93	1.480	Orians (1980)
Westham Island	2	4.80	0.020	Picman, Can. J. Zool. 58:337–350, 1980
Chesapeake Bay: Colony 1	4	1.47	0.063	Meanley and Webb (1963)
Chesapeake Bay: Colony 2	3	1.63	0.063	Meanley and Webb (1963)
Airport Marsh	2	2.15	0.168	Case and Hewitt (1963)
Inlet Valley Marsh	2	2.17	0.000	Case and Hewitt (1963)
Millbrook Marsh	5	1.48	0.578	Brenner, Am. Midl. Nat. 76:201–210, 1966
Lake Opinicon, Ontario	2	2.80	0.051	Weatherhead and Robertson, Can. J. Zool. 55:1201–1267, 1977
87th St. Slough	2	2.17	0.054	Lenington and Scola, this study
Redwing Slough	2	5.61	8.860	Lenington and Scola, this study

neither of these factors can account for the decrease in harem size on Redwing Slough between 1974 and 1978 because territories did not differ in size between the two years and mean cattail density was substantially greater in 1978 than in 1974. No other components of reproductive success (clutch-size, nesting success, or number of young fledged from successful nests) differed significantly between 1974 and 1978.

It is possible that the change in harem size on Redwing Slough between 1974 and 1978 simply represents normal between-year variability. To test this hypothesis we examined published data from all marsh localities (Table 2) where red-wing harem sizes have been recorded for two or more years in order to estimate the between-year variance in harem size. The variance in 13 localities ranged from 0 (Case and Hewett, Living Bird 2:7–20, 1963) to 1.48 (Orians, Some Adaptations of Marsh-nesting Blackbirds, Princeton Univ. Press, Princeton, New Jersey, 1980). The variance in harem size on Redwing Slough was 8.86. The

probability of obtaining one value more extreme than the 13 others if they all come from the same population is $1/2^{12}$ or 0.00025. Thus, it is highly unlikely that the decrease in harem size in Redwing Slough is due to nothing more than normal between-year variation.

In a study of interactions between red-wings and grackles nesting on a cattail marsh Wiens (1965) concluded that red-wing female reproductive success was not adversely affected by the presence of grackles on the marsh. This conclusion was supported by Snelling (Auk 85:560–585, 1968), whose data suggested that red-wings and grackles do not compete for food. Although Wiens did not have data on harem size before and after the arrival of grackles on the marsh, far fewer nests were found on his marsh during the years of his study than had been found 15 years earlier when no grackles nested on the marsh (Beer and Tibbits, Flicker 22:61–77, 1950). Data from this study support the contention of the above two studies that female reproductive success may not be decreased by the presence of grackles. If, however, female red-wings consider marshes containing grackles undesirable places to nest, reproductive success of male red-wings would be considerably reduced due to the decrease in harem size. On Redwing Slough the mean number of young fledged per male was 9.8 in 1974 and 5.1 in 1978. As one might expect, male red-wings in this study, as well as on the marsh studied by Wiens (1965), were aggressive toward grackles.

It is not, however, evident why female red-wings should avoid nesting on marshes containing grackles. One possible reason for this avoidance may be the predatory behavior of grackles noted by several authors (Davis, Auk 61:139–140, 1944; Poor, Proc. Linn. Soc. N.Y. 54-57:54–55, 1946; Bent, U.S. Natl. Mus. Bull. 211:1–549, 1958; Meanley and Webb, Chesapeake Sci. 4:90–100, 1963). Although there was no evidence in either this study or that by Wiens (1965) that grackles preyed on red-wing nests, Meanley and Webb (1963) considered grackles to be the principal predators on red-wing nests in the Chesapeake Bay region. This behavior on the part of grackles may result in aggression on the part of red-wing males toward grackles attempting to nest on a marsh and female avoidance of nesting in marshes containing grackles. Because it would probably be impossible for red-wings to know in advance whether or not in any given instance grackles would or would not prey on nests, the agonistic behavior of red-wings toward grackles may be manifested even in situations in which grackles represented little or no threat to red-wing nesting success. The aggressive behavior of the male might further contribute to the decrease in harem size since males would have less time to court females.

We thank P. H. Stepney and an anonymous reviewer for very helpful comments on an earlier draft of this manuscript.—Sarah Lenington, *Institute of Animal Behavior, Rutgers Univ., 101 Warren Street, Newark, New Jersey 07102* and Rose Scola, *Brookfield Zoological Park, Brookfield, Illinois.* *Accepted 20 Feb. 1981.*

Wilson Bull., 94(1), 1982, pp. 93–95

Incidence of Brown-headed Cowbird parasitism on Red-winged Blackbirds.—A high incidence of Brown-headed Cowbird (*Molothrus ater*) parasitism on the Red-winged Blackbird (*Agelaius phoeniceus*) appears to be a localized phenomenon (Friedmann, The Cowbirds, Charles C. Thomas Co., Springfield, Illinois, 1929). Friedmann et al. (Smithson. Contrib. Zool. 235, 1977) report that the incidence of parasitism on red-wings is greatest in the central United States and Canada. Within this geographic region the literature shows a wide range in rates of parasitism. Berger (Wilson Bull. 63:26–35, 1951) reported that only 5% (N = 99) of the red-wing nests he examined in Michigan contained cowbird eggs, and Wiens (Wilson Bull. 75:130–138, 1963) observed no parasitism in 33 nests in southern Okla-

Table 1
Number of Red-wing and Cowbird Eggs

	Total nests	Red-wing eggs/nest	Nests with cowbird eggs (no. of eggs)				
			0	1	2	3	>3
	26	0	0	17	5	2	2 (4, 4)
	34	1	23	2	7	1	1 (6)
	34	2	22	6	5	1	
	64	3	32	22	4	5	1 (9)
	92	4	65	18	7	1	1 (7)
	8	5	7	1	0	0	
Totals	258		149	66	28	10	5

homa. In Nebraska, however, Hergenrader (Auk 79:85–88, 1962) found that 54% (N = 59) of the Red-winged Blackbird nests were parasitized and had 1–3 cowbird eggs per nest.

While banding red-wings in conjunction with a blackbird-sunflower project, we found 258 red-wing nests during May and June 1979. All nests were in cattails (*Typha* spp.) in roadside ditches in Cass County, North Dakota. Of the 258 nests, 109 (42%) contained at least one cowbird egg. Of the parasitized nests, 61% had one cowbird egg; 26% had two; 9% harbored three cowbird eggs (Table 1). Two of the parasitized nests had no red-wing and four cowbird eggs. Three other nests had red-wing to cowbird egg ratios of 1:6, 4:7 and 3:9. We flushed the female red-wing off the 3:9 nest. The eggs were warm, indicating that incubation was in progress. Friedmann (U.S. Natl. Mus. Bull. 233, 1963) reports that using all available data, 60% of all parasitized nests contain one cowbird egg.

Using calculations given by Mayfield (Condor 67:257–263, 1965), our sample does not show a random distribution of cowbird eggs. Looking at all nests and combining nests with more than four cowbird eggs in order to maintain adequate cell size, $\chi^2 = 50.8$ and randomness is rejected at the $P < 0.0001$ level (df = 5). Using just the subsample of parasitized nests and combining all nests with more than five cowbird eggs, $\chi^2 = 42.7$ and randomness is rejected at the $P < 0.001$ level (df = 5). Mayfield used figures adjusted for desertion to show that some rejected groups actually fit a random distribution. For these calculations, however, he excludes data from species with other mechanisms of defense besides desertion, which includes Red-winged Blackbirds.

One curious aspect about cowbird parasitism on red-wings is the variability in the percentage of affected nests. Red-wings are accepter species (Friedmann et al., 1977) but also are markedly aggressive towards cowbirds, often mobbing in groups (Robertson and Norman, Can. J. Zool. 55:508–518, 1977). Robertson and Norman (1977) found significantly higher rates of parasitism in low density populations in which the aggressive behavior towards cowbirds may only serve to notify cowbirds of the location of red-wing nests. Friedmann (1963) reports that red-wings are less parasitized in cattail marshes than in upland bushes and that most parasitism in marshes occurs on the perimeter of the marsh.

Like Hergenrader (1962), we found a high incidence of parasitism in roadside ditches. The ratio of perimeter area to the total area of nest habitat in roadside ditches is large. This factor, combined with low red-wing densities, may have contributed to the high incidence of parasitism and the non-random distribution of cowbird eggs in our sample. Information comparing parasitism in large continuous marshes and roadside strips of marsh would be of value in further clarifying red-wing/cowbird relationships.

John Cummins and Lonnie Mettler assisted in the field. We thank W. J. Bleier and J. F. Cassel and anonymous reviewers for helpful comments on this note. This research was part of Project 14-16-0009-79-037 from the U.S. Fish and Wildlife Service to the North Dakota Agriculture Experiment Station (R. B. Carlson, Principal Investigator).—GEORGE M. LINZ, *Dept. Zoology, Stevens Hall, North Dakota State Univ., Fargo, North Dakota 58105* AND SUSAN B. BOLIN, *Dept. Biology, Foster Hall, New Mexico State Univ., Las Cruces, New Mexico 88003.* *Accepted 11 Feb. 1981.*

Wilson Bull., 94(1), 1982, pp. 95–96

Western Kingbird nests in abandoned woodpecker cavity.—Most nests of the Western Kingbird (*Tyrannus verticalis*) are in trees against the trunk, in a crotch, or on a horizontal branch (Harrison, A Field Guide to Western Birds' Nests, Houghton Mifflin Co., Boston, Massachusetts, 1979). Some Western Kingbird nests are placed on towers, buildings, or utility poles (Bent, U.S. Natl. Mus. Bull. 179, 1942). Eastern Kingbirds (*T. tyrannus*) occasionally nest on hollowed tops of fence posts or dead stubs (Pettingill, Jack-pine Warbler

FIG. 1. Adult Western Kingbird at its nest in an abandoned woodpecker cavity, Dunn County, North Dakota.

51:124–126, 1973; Hamas, Jack-pine Warbler 57:26–27, 1979), and there is at least one report of a Western Kingbird placing a nest atop a hollow tree stump (Bent 1942).

On 6 July 1980, I found a Western Kingbird nest in an abandoned woodpecker cavity in Dunn County, North Dakota (Fig. 1). The nest was in a dead plains cottonwood (*Populus sargentii*) in the floodplain of the Little Missouri River, where a dense forest of mature cottonwood and green ash (*Fraxinus pennsylvanica*) trees had been killed several years earlier by high water resulting from an impoundment. Dominant living vegetation around the nest tree consisted mostly of willow (*Salix* spp.) shrubs, especially sandbar willow (*S. interior*) and heart-leaved willow (*S. cordata*). Both Western and Eastern kingbirds were abundant in this habitat, which was apparently ideal for both species because of the numerous dead trees that served as foraging perches.

I observed at least two kingbird nestlings in the nest cavity on 6 July and several dates thereafter. The adults fed the young and removed excreta by perching at the cavity entrance and leaning into or entering the cavity. The cavity entrance was 2.3 m above ground, measured 12 cm high and 8 cm wide, and faced SSW. The interior of the cavity was 10 × 12 cm and the outside diameter of the tree at the height of the nest was 19 cm. The cavity extended 5 cm below the bottom of the entrance, though much of this space was filled with nesting material so that the nest contents were level with the bottom of the entrance. The cavity was probably excavated by a Common Flicker (*Colaptes auratus*), the most common woodpecker in the area.

I have not been able to locate any other records of Western Kingbirds nesting in abandoned woodpecker cavities.—Benedict C. Pinkowski, *Fort Berthold College Center, New Town, North Dakota 58763.* *Accepted 23 Feb. 1981.*

Wilson Bull., 94(1), 1982, p. 96

Piracy by a Great Black-backed Gull on a shark.—Avian piracy or kleptoparasitism has been extensively reviewed by Brockmann and Barnard (Anim. Behav. 27:487–513, 1979). Piracy by gulls on other bird species is common but piracy on other animals has seldom been reported. On 7 August 1977, a Great Black-backed Gull (*Larus marinus*) was seen robbing a shark about 60 m west of Eastern Egg Rock, Muscongus Bay, Maine. Three sharks were observed for 30 min in calm seas swimming slowly at the surface with both their dorsal and caudal fins visible. I used lobster pot buoys and cormorants (*Phalacrocorax auritus*) as scales, to estimate that the sharks were 1.7–1.8 m long. One shark splashed the surface with its caudal fin as it turned sharply entering a school of pollock (*Pollachius virens*). Three Great Black-backed Gulls immediately flew to the area. During one sharp turn the shark lifted its head out of the water revealing a 25 cm pollock. A gull dropped to the water in front of the shark, pulled the pollock from the shark's mouth and flew off. The shark then resumed its sluggish swimming. The locality, size, shape, manner of surface swimming and food suggested a mackerel shark or porbeagle (*Lamna nasus*).

These observations were made while working for the Fratercula Fund of the National Audubon Society under the direction of S. W. Kress.—Thomas W. French, *New York Cooperative Wildlife Research Unit, U.S. Fish and Wildlife Service, Cornell Univ., Ithaca, New York 14853.* *Accepted 20 Feb. 1981.*

Wilson Bull., 94(1), 1982, pp. 97–103

ORNITHOLOGICAL LITERATURE

Form and Function in Birds, Vol. 2. By A. S. King and J. McLelland (eds.). Academic Press, London (U.S. edition published by Academic Press Inc., New York, New York), 1981:xi + 496 pp., numerous black-and-white photos and line drawings. $97.00.—This is the second in a projected three-volume series on the functional anatomy of birds. As in volume 1, which was reviewed earlier, the emphasis is on thorough descriptive anatomy as the basis for functional analysis at a non-biochemical level. There is a strong coverage of reproduction in this volume, with chapters on the male genital organs (P. E. Lake) and on the cloaca and phallus (A. S. King). Other chapters cover the endocrine glands (R. D. Hodges), cardiovascular system (N. H. West, B. Lowell Langille, and D. R. Jones), lymphatic system (M. E. Rose), and cranial nerves (A. Bubień-Waluszewska). These are mostly lengthy chapters giving much more anatomical detail than the coverage provided in "Avian Biology." In most cases there is a strongly comparative aspect with the conditions in various kinds of birds as well as reptiles being considered. Nevertheless, the limitations of the primary literature often make it impossible to avoid a strong emphasis on a few domestic species. The final chapter is a concise account of the functional anatomy of the jaw apparatus by P. Bühler. It is quite short (30 pp.) by the standards of this series, giving a descriptive account of the morphology of the jaw apparatus followed by an analysis of its kinetics. The discussion is based heavily on Bühler's own work on caprimulgids, but with numerous references to other studies. Despite this, the account is general rather than comparative, and does not review the diversity of avian jaw mechanisms. A fuller appreciation of the avian feeding mechanism may be obtained by reading Bühler's chapter in conjunction with the section on the oral cavity and pharynx in J. McLelland's chapter on the digestive system in volume 1 of this series, which includes discussions of the tongue, oral sacs, salivary glands, taste buds, bill, and deglutition.

This book continues the high level of scholarship established in volume 1, but unfortunately the price will again put it beyond the reach of most of those who would benefit from owning their own copy.—Robert J. Raikow.

Behavioral Mechanisms in Ecology. By Douglass H. Morse. Harvard University Press, Cambridge, Massachusetts, 1980:383 pp., 99 numbered text figs., 3 tables. $25.00.—Hitherto, there has never been an adequate text on behavioral ecology, but Douglass Morse's book goes a long way towards filling this gap. Although this book does not deal only with birds, well over half of the studies described concern birds. This does not merely reflect the author's bias, but rather the suitability of birds for field studies of behavior.

The book opens with three chapters on foraging behavior, and provides a useful and original review of this best-studied aspect of behavioral ecology. Other topics treated include habitat selection, predator avoidance, thermoregulatory behavior, reproduction, competition for mates, territoriality, spacing patterns, competition between species and social groups. Most chapters conclude with a useful 'synthesis' section, and the final chapter attempts to look ahead to future developments. The literature coverage is broad and cosmopolitan and I found the treatment well-balanced and fairly easy to read. There are, however, one or two surprising omissions. Brood parasitism is not discussed and coevolution in general gets little attention.

The layout of the book is clear and the figures adequate, though unimaginative. (Maybe imagination is too costly, for the price of the book is quite reasonable!) The book contains few errors and stresses empirical evidence, rather than fashionable theorizing, although theoretical issues are considered extensively. Most examples are given in limited detail, but

I sometimes wished for more detail on fewer examples and more enthusiasm for particularly significant studies. Overall, Morse is quite successful at walking the tightrope between excessive detail and conceptual clarity.

The book is a good introduction to the literature on behavioral ecology and should make a suitable text for advanced college courses, as well as providing an accessible account of the field to all students of natural history. There is, however, one respect in which the book differs from the average text. Morse has chosen to include a lot of material from his own studies on flocking and resource partitioning in birds. This is indeed significant work, and it has been skilfully integrated into the appropriate chapters, but it makes the book a partial hybrid between a text and a monograph. Despite my minor reservations, this is clearly the best text yet written on behavioral ecology. It contains both a useful survey of the field and a critical and perceptive look to the future.—JAMES N. M. SMITH.

BIRDS OF PREY OF THE WORLD. By Friedhelm Weick. Paul Parey, Hamburg and Berlin, 1980:159 pp., 40 color plates, many line drawings. Text in German and English. $48.00.—Friedhelm Weick of Bruchsal, West Germany, has long been fascinated by the diurnal birds of prey. When he first saw Peter Scott's admirable "Coloured Key to the Waterfowl of the World" in 1967, Weick conceived the idea of doing a similar book on the Falconiformes. He was commissioned to illustrate volume 4 (1971) of the "Handbuch der Vögel Mitteleuropas" (Glutz von Blotzheim, ed.), an assignment that gained him valuable experience in drawing raptors. There are only three color plates in that book, a pretty good one of Bonelli's Eagle (*Hieraaetus pennatus*), a pretty bad one of the Red-footed Falcon (*Falco vespertinus*), and a painting of study skins of two races of *Buteo buteo*. The text, however, is liberally illustrated with line drawings. Many of these were adapted from photographs, and it is clear that the experience of preparing these drawings gave Weick a good feel for postures and proportions of birds of prey. In his new book, the color plate figures are in the stylized field guide tradition, all standing or perched and facing left. In spite of these constraints, Weick has managed to capture remarkably successfully the *Gestalt* of each of the various groups. His main fault is a tendency to draw heads overly large in some groups (*Accipiter* on pl. 21; several plates of *Buteo*; some of the kites on pls. 3–5).

Although the plates are crowded with figures, the large format permits the individual birds to be portrayed in good detail. The coloring is anything but subtle, and there is a marked tendency to exaggerate color contrasts: the sea-eagles (pl. 6) and many others look much too scaly, and the tail barring of *Milvus* kites on pl. 5 is far more conspicuous than in any specimens I have examined. Reddish colors tend to be exaggerated (see adult ♂ Merlin [*Falco c. columbarius*], pl. 37, and all figures of Red-shouldered Hawk [*Buteo lineatus*], pl. 24). All of these faults are relatively minor, and are greatly outweighed by the comprehensiveness of Weick's work. He has illustrated all of the species and most of the subspecies of Falconiformes, adding immatures, color phases, and both sexes as appropriate, thus providing a truly significant contribution to the iconography of the order.

The plate captions, which, like the text, are in parallel German and English columns, have been reduced to an extent that may drive some readers to the point of getting new eyeglass prescriptions. This reduction has permitted the inclusion of a tremendous amount of information: scientific name (with author and date), German and English names, characters of species and subspecies, distribution, standard measurements, and weight. Taxa illustrated are named in boldface, those not figured are in ordinary type. Spot-checking reveals a few discrepancies between captions and plates hardly unexpected in a work of this magnitude. There is a figure of *Falco columbarius subaesalon*, although the caption typeface would indicate otherwise. A figure of a Peregrine (*F. peregrinus*) on pl. 40 is labelled only "♂ adult" with no subspecies name, but appears probably to represent the adult female of *F. p.*

japonensis. The characters of the very dark race *F. p. pealei* are given only as "Proportionally longer and broader tailed" (than what?). No subspecies of Philippine Falconet (*Microhierax erythrogonys*) are listed in the caption of pl. 35, but figures are provided for the nominate race and for *M. e. meridionalis*. However, the latter is shown as having buffy rather than white flanks, whereas the two races differ only in size (Parkes, Nemouria 4:3–4, 1971). The scale is too coarse to show size differences well. The smallest *Buteo* in the world is the Isla Cozumel race of Roadside Hawk (*B. magnirostris gracilis*); size is not mentioned as a character of the race, and it is figured the same size as a race that averages 35% heavier.

For two species, the Madagascar Serpent Eagle (*Eutriorchis astur*) and New Britain Grey-headed Goshawk (*Accipiter princeps*), Weick has provided an outline figure to stand in for the unknown immature plumage. There may well be other tropical forms of which the immature plumages are unknown, and it is a certainty that plumage sequences in many are poorly understood, as exemplified by the Fishing Buzzard (*Busarellus nigricollis*), a fairly common Neotropical species that has a plumage stage that I have never found figured or described in the literature.

The first 62 pages of the book constitute the text, liberally illustrated with line drawings. The birds are arbitrarily divided into six size classes, with figured examples, from very small (*Microhierax*) to very large (*Vultur*). There are the usual diagrams of topography and of standard measurements. A useful table lists the plates drawn to each of seven size-scales; although the actual scale ratio is not given, at least one knows which figures may be compared directly.

Pages 15–40 are devoted to a "Key for identifying." A true key should ideally be dichotomous, and should at least present contrasting characters. Weick's "key" would probably take as long to use for identification as would flipping through the plates. In the first part of the "key" the species are divided by the six size classes, with brief descriptions of each species. Oddly, the classes are not given in size sequence, but as very large, large, rather large, very small, small, and medium-sized. Appropriate species are then grouped under a series of non-contrasting characteristics: first those with long necks, then those with long tarsi, areas of bare skin on head, head and neck naked, bill yellow, bill red, "conspicuous shapes of bill" (six categories), three groups of cere colors, four groups of iris colors, three groups of leg colors, "big head, large eyes," different shapes of crest, conspicuous tail shapes, and six plumage color categories, some of which seem arbitrary or even inappropriate.

A "Compendium of the order Falconiformes" follows, in which suprageneric categories are listed and genera described and illustrated. Again, the characters by which the genera are identified are all too often non-contrasting. For example, *Haliastur* is characterized as having the outer toe larger than the inner, but relative toe proportions are given for no other genus of kites nor for the related sea-eagles. Thus, the generic descriptions do describe the members of the genus, but do not define them in relation to other genera. Each such description is accompanied by a line drawing of the head and often the foot of a typical member of the genus.

Indices are provided for German, English, and scientific names of birds. The latter index has a useful feature in that synonymized genera are included (although not mentioned in the text) and their equivalencies given.

The book ends with an "Annotated bibliography," which, unfortunately (and contrary to the rest of the book) shows every sign of careless preparation. For one thing, it is not "annotated" in the least. It is loaded with misspelled names and wrong initials of authors ("Amodon," "Friedman," "G." R. Blake) and erroneous or incomplete citations. Mayr is wrongly given as coauthor of Delacour's "Birds of Malaysia" and the date given as 1971 instead of 1947. The Bent "Life histories" volumes are attributed to "Bull. US Nat. Mus.

New York." Pagination and publishers' names are given or omitted at random. Regional works consulted were not always the most recent; thus, Delacour and Mayr (1946) and Herklots (1961) are listed for the Philippines and Trinidad respectively, but duPont (1971) and ffrench (1973) are omitted.

It is understandable that the author could not consult all pertinent periodical literature as well as standard regional works and check-lists. Although the Preface is dated "Spring 1980," Weick had obviously finished his manuscript before the 1979 publication of the revision of volume I of the "Peters" check-list, as he omits such relatively recently described forms (all listed in "Peters") as *Aviceda leuphotes wolfei* Deignan, 1948; *A. l. andamanica* Abdulali, 1970; *Melierax canorus argentior* Clancey, 1960; *Accipiter virgatus quagga* Parkes, 1973; *Falco sparverius nicaraguensis* Howell, 1965; and a number of others. Weick also overlooked Monroe's demonstration (Ornithol. Monogr. 7:80–82, 1968) of the specific distinctness of *Buteogallus anthracinus* and *subtilis*, and Schwartz's parallel finding (Condor 74:399–415, 1972) that *Micrastur gilvicollis* and *ruficollis* are separate species, both "splittings" accepted by Stresemann and Amadon in "Peters."

As a summary of the Falconiformes, Weick's text may prove to be more useful than I have suggested here, but there is no doubt that his meticulously prepared illustrations represent a major accomplishment. For these alone, this book belongs in ornithological reference libraries in general, as well as in libraries of raptor specialists. Its cost is by no means out of line with current book prices, especially in view of its many color plates.—KENNETH C. PARKES.

THE MERLINS OF THE WELSH MARCHES. By D. A. Orton. David and Charles, Inc., North Pomfret, Vermont, 1980:168 pp., 8 black-and-white plates with captions. $18.50.—In the 1950's and 60's, it became evident that the population of Merlins (*Falco columbarius*) in the Welsh countryside had been depleted just as it had in other areas of the world where organochlorines were in use. In the early 70's, these birds began to reappear in limited numbers. It was at this time that D. A. Orton and his associates ferreted a small section of Welsh moorland for four consecutive seasons in order to discover as many nesting pairs of this tiny falcon. Orton, a retired business executive, amateur ornithologist, and novice Merlin watcher (at least initially) made repeated day-long visits to the nests on weekends and other holidays. From carefully detailed notes, he presents various aspects of the Merlin breeding cycle beginning with courtship in mid-April and concluding with young on the wing in late June. Although centered on nesting Merlins, there is considerable description of behavior by other species in the area of observation, including Kestrels (*Falco tinniculus*) and even Hobbies (*Falco subbuteo*).

The book is of a popular nature seasoned with subtle humor. The style of presentation is that of an adventure series or even a mystery which covers Orton's field experiences year by year, trip by trip. One frequently wonders what will occur during his next visit to the nesting area or whether the young will be alive at all.

Orton continually asks questions about everything he observes in the field, and he frequently derives conclusions from even singular observations, a liberty associated with this style of writing. He makes a habit of putting into print the type of interrogative supposition which all field biologists ponder in their own minds, but because of strict training, fail to state aloud. Initially, some of these suppositions which I considered to be totally erroneous were disturbing, but I later found this approach somewhat intriguing. Orton does not portray himself as an omniscient authority, and in fact with the close of his book he states that "the time has arrived for the ball to be passed from the observant amateur to the professional scientist . . . to do the whole of the job as it needs to be done."

This book will be appreciated by every biologist who has spent any time at all in the field.

The author seems to really enjoy his day-long field excursions and relates experiences ranging from interesting observations of Whinchats (*Saxicola rubetra*) to the sometimes trying and wholly unpleasant weather conditions experienced in the field. For example, during a severe hail storm he first expressed his concern for the brooding adult falcon and her downy young, but soon admitted that he forgot all about the Merlins out of concern for his own welfare.

Although this work does not present vast quantities of new information on Merlin behavior, both falcon enthusiasts and serious students alike will want to review Orton's observations. I found the book to make pleasurable reading.—Steve Sherrod.

Hacking: A Method for Releasing Peregrine Falcons and Other Birds of Prey. By Steve K. Sherrod, William R. Heinrich, William A. Burnham, John H. Barclay, and Tom J. Cade. The Peregrine Fund, 1424 N. E. Frontage Rd., Fort Collins, Colorado 80524, 1981:61 pp., 16 figs., paper cover. Price not given.—A detailed manual of the methods used by The Peregrine Fund to release young peregrines into the wild as part of its program to restore natural populations. At least some of the information is probably useful with other species as well.—R.J.R.

Birds of East Africa: Their Habitat, Status and Distribution. By P. L. Britton (ed.). East Africa Natural History Society, Nairobi, Kenya, 1980:271 pp., 4 color plates, 8 black-and-white plates, 4 maps. $17.00. The Breeding Seasons of East African Birds. By L. H. Brown and P. L. Britton. East Africa Natural History Society, Nairobi, Kenya, 1980:164 pp., 2 maps. $15.00.—These two volumes were published by the East Africa Natural History Society to commemorate the Society's 70th anniversary in 1979. They cover the area of Uganda, Kenya and Tanzania, which includes the most complex topography in Africa and practically all vegetation types known from that continent; a total of 1293 species are recorded, roughly 15% of the known bird species.

The "Birds of East Africa" emphasizes distribution by species, although distribution details for all subspecies are given throughout. The relationship between species is stressed, and liberal use is made of the superspecies concept. The introduction contains detailed descriptions of the topography, climate and vegetational zones, without a knowledge of which the distributions would make no sense. Of particular value are the definitions of various habitats such as woodland, bushland, thickets, etc., which have been used loosely and ambiguously in the past. The distributional notes contain an enormous amount of detail that has been scattered through the literature of the last 50 years, and its compilation must have been a formidable task. The authors are to be congratulated for persevering in their undertaking and making this material available in one place. The four attractive color plates by Rena Fennessy feature many of the East African endemics.

"The Breeding Seasons" is likewise a major contribution which includes not only published records but those from the EANHS nest-record card scheme. Altogether 86,331 dated records were available, not counting those for colonial species like *Quelea quelea* for which there are literally millions. However, as in all tropical countries, the coverage was spotty. Dated records for only 861 of the 1123 resident species exist, and of these 861 only 422 had more than 10 records. Because of the complexities of topography and rainfall patterns, the area was divided into five climatic regions, defined by the presence of one or two rainy seasons per year, and by the period of the year in which they fall. In the individual species accounts, the records are listed by months under each region, which further dilutes the available data for any one region. However, there is still a vast array of breeding data for East Africa that is available nowhere else, and the general discussion of tropical breeding seasons that concludes the book will be of interest to any student of tropical birds.

The EANHS is to be congratulated for their two anniversary volumes. The only unhappy

note is that my expectation that two lists published by the same society and sharing an author would follow the same order was unfulfilled. "Breeding Seasons" follows the systematic order of White (Revised Check-list of African Birds, 1961–1965), while "Birds" has genera and species listed alphabetically within families. However, this is a minor defect in two books that anyone studying African birds should have.—Melvin A. Traylor, Jr.

Birds of the Carolinas. By Eloise F. Potter, James F. Parnell and Robert P. Teulings. The University of North Carolina Press, Chapel Hill, 1980:viii + 408 pp., 338 color photographs (321 of birds and 17 of habitats), end paper maps, 1 black-and-white drawing. $14.95.—This reasonably priced book summarizes the latest information on the bird life of North and South Carolina. Brief introductory chapters cover bird identification, migration through the Carolinas, the annual cycle, habitats, and conservation. Species accounts for 415 species are included in 335 pages of text followed by a five page glossary, two pages of suggested readings, and a six page index of vernacular bird names.

Each species account includes the vernacular and scientific names, the range of lengths (and for some pelagic species the wing span) measured in inches and centimeters, and four principal subheadings: range, nesting habits, feeding habits, and description. "Range" contains information on seasonal abundance, residence status, and distribution in the Carolinas, while nesting habits are mentioned only for species breeding in the two states. The species descriptions are brief and are not provided for those species having hypothetical status of occurrence. Although the color photographs are quite good in general and may be helpful for identification, they are no substitute for field guide illustrations. Several species have no photographs, and for other species only one sex is pictured.

The most notable omission in the book is information on vocalizations. Only when calls or songs are critical to the identification of two similar species is mention made of vocalization. Despite this and some other minor shortcomings, the authors are to be congratulated for producing an informative and attractive book. The publisher also deserves kudos for the affordable price it is asking for a volume containing so much color.—Sidney A. Gauthreaux, Jr.

A Field Guide to the Bird Songs of Britain and Europe, Record 15. By Sture Palmer and Jeffrey Boswall. The Swedish Radio Co. (Sveriges Riksradio AB), Stockholm, Sweden, 1981. Price not given.—This 12-inch 33⅓ r.p.m. phonograph record includes vocalizations of 54 species. It is a supplement to a series of the same title published between 1969 and 1973 comprising 14 discs. The entire series of fifteen provides recordings of 585 species. This disc (No. RFLP 5015) and the earlier ones may be ordered from Conifer Records, Horton Road, West Drayton, Middlesex UB7 8NP, England.—R.J.R.

The Mystery of Migration. By Robin Baker, Chief Contributing Editor. The Viking Press, New York, 1981:256 pp., many color photos and drawings, many black-and-white photos and drawings. $29.95.—This attractive volume is an American edition of a book produced in England. It was compiled by a six-person board of contributing editors with no actual authors given. In many ways, particularly with its mixture of text, diagrams, drawings, and photos it resembles one of the LIFE publications of past years. Twelve chapters cover the subject of migration in general, and then consider in detail the migration of plants, invertebrates, insects, fish, amphibians and reptiles, birds, bats, aquatic mammals, land mammals, and man. These discussions are at the level appropriate for the general audience but are nonetheless quite accurate and informative.

The chapter on birds is the longest in the book and is up-to-date and quite thorough. The migration patterns in both the Old and New worlds, as well as those of seabirds, are dis-

cussed. Both the techniques of migration study as well as the various theories of bird navigation are discussed. However, it is not emphasized that a migrating bird is probably able to use more than one navigational system as required by conditions.

I consider this book to be highly desirable in school libraries, and it would make a suitable present for young students beginning to be interested in nature. The ornithologist who has been studying migration will find little of value but other ornithologists might find interesting reading, particularly in the non-bird chapters.—George A. Hall.

The Illustrated Bird Watcher's Dictionary. By Donald S. Heintzelman. Winchester Press, P.O. Box 1260, 1421 South Sheridan, Tulsa, Oklahoma, 1980:164 pp., numerous photographs of varying quality, a few unnumbered text figs. $11.95.—Webster (and he should know) defines a dictionary as "A reference book listing terms or names important to a particular subject or activity along with a discussion and their meanings and applications." This book does little more than list terms and names. The text which follows each entry is often incorrect or unclear. Contrary to what Heintzelman states, S. F. Baird was not the first secretary of the Smithsonian. I believe that careful searching will reveal that Joseph Henry had that distinction (and he's not even listed in the book, although his statue is in front of the Smithsonian). Some of the definitions border on inane (e.g., "Bufflehead—a small North American Duck," hardly descriptive and definitely applicable to at least 10 other species. Or how about "Altricial—born requiring nourishment," as opposed to . . . ?).

Many of the "biographical" entries are not only incomplete, but border on humorous (with a little digging). Examples include: Thomas Stewart Traill, "A friend of John James Audubon and respected British citizen . . ." (we find that Audubon had many friends and most are listed). William Swainson, "An English naturalist who roamed widely . . . ," Percy Tavener, "A well known Canadian ornithologist who wrote extensively about Canadian birds" (what else?). We are also told that John Bachman's daughter married John Audubon's son (isn't that nice).

The book is vintage Heintzelman, heavily slanted towards hawks and hawk watching. Thirteen lines are given to Accipiters, three words to Alcedinidae, Alcidae, Turdidae, etc. He coins many new terms not found in dictionaries (even unabridged), such as "falconiformologist" (which should make Clay White and his raptor "groupies" proud). A further example of bias is the fact that seven lines are given for Heinz Meng (meaning no disrespect to Dr. Meng), but only 2½ lines for S. F. Baird and five words for Alexander Wilson.

Not only is the book sadly lacking in the coverage of everyday terms, some key items are completely ignored. For example, in the appendix "National Bird Watching and Ornithological Organizations," the Cooper Society is not even mentioned.

The only really interesting entry in the book is listed under C. A. Allen, "An American field ornithologist and collector of birds," which confirms the belief held by many that these two professions are, in fact, different (perhaps mutually exclusive?).

In sum, this book might make good reading for someone with interests in elementary birding, but for anyone else it is definitely a waste of money. I have hidden my review copy behind a cherished edition of the Official Encyclopedia of Baseball given to me by Jon Barlow.—Robert C. Whitmore.

ORNITHOLOGICAL NEWS

AARON M. BAGG STUDENT MEMBERSHIP AWARDS

Student Membership Awards in The Wilson Ornithological Society have been made available through funds generously donated in memory of Aaron M. Bagg, a former president of the society. The Student Membership Committee has made the 1981 awards to the following students: Anthony H. Bledsoe, Yale Univ., Connecticut; Petra G. Bohall, Univ. Florida; Bruce A. Colvin, Bowling Green State Univ., Ohio; William E. Davis, Univ. California-Davis; James G. Devereux, Frostburg State College, Maryland; Sharon Goldwasser, Univ. Arizona; Michael E. Kaspari, Univ. Nebraska; Francis P. Kehoe, Univ. Western Ontario; Mary C. McKitrick, Univ. Pittsburgh; Mari B. Smaby, North Dakota State Univ.; Ellen J. Snyder, Univ. Maine-Orono; Robert E. Szafoni, Univ. Illinois; Brian M. Winter, Iowa State Univ.

John L. Zimmerman, *Chairman*

WILSON SOCIETY COMMITTEES

The Officers of the Society would like to broaden the participation of the membership in its operation and urge individuals who would be willing and interested in serving to make themselves known. Standing committees of the Society include: Conservation, Endowment, Library, Membership, Research and Student Membership. If you would like to serve on any of these committees in the future please contact the Chairman of the Nominating Committee, Dr. George Hall, Dept. Chemistry, West Virginia University, Morgantown, West Virginia 26506.

TAMAULIPAN BIOTIC PROVINCE SYMPOSIUM

An international symposium will be held on the Tamaulipan Biotic Province, 28–30 October 1982, in Corpus Christi, Texas. All ecological aspects of the biome will be covered: vegetation, invertebrates, vertebrates, ecological structure and function, biological resources (use and effects) and management, as well as aspects of applied science and conservation. Interested paper contributors should submit abstract by 1 August 1982; invited-paper abstracts must be received by 1 September 1982. Contact Gene Blacklock, Curator, Welder Wildlife Foundation, P.O. Drawer 1400, Sinton, Texas 78387; or David Riskind, Head, Resource Management Section, Texas Parks and Wildlife Dept., 4200 Smith School Rd., Austin, Texas 78744 for information on papers. Contact Jimmie Picquet, Director, John E. Conner Museum, Texas A&M Univ., P.O. Box 2172, Kingsville, Texas 78363 for registration information.

ANNOUNCEMENT AND CALL FOR PAPERS

The sixth annual meeting of the Colonial Waterbird Group will be held 4–7 November 1982 in Washington, D.C. A symposium on the feeding biology of waterbirds is planned. Papers given at the meeting are eligible, after refereeing, for publication in Colonial Waterbirds. Anyone wishing to contribute to either the symposium (deadline 1 Sept.) or general session (deadline 15 Sept.) should contact Dr. Michael Erwin, U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, Maryland 20708. Information concerning registration can also be obtained from Dr. Erwin.

The Wilson Bulletin

Editor Jon C. Barlow

Department of Ornithology
Royal Ontario Museum
100 Queen's Park
Toronto, Ontario, Canada M5S 2C6

Associate Editor Margaret L. May

Assistant Editors Gary Bortolotti
Nancy Flood
Keith L. Bildstein

Senior Assistant Editor Richard R. Snell

Editorial Assistants C. Davison Ankney
James D. Rising

Review Editor Robert Raikow
Department of Biological Sciences
University of Pittsburgh
Pittsburgh, PA 15260

Color Plate Editor William A. Lunk
865 North Wagner Road
Ann Arbor, MI 48103

Suggestions to Authors

See Wilson Bulletin, 91:366, 1979 for more detailed "Suggestions to Authors." Manuscripts intended for publication in *The Wilson Bulletin* should be submitted in triplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411–419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

Notice of Change of Address

If your address changes, notify the Society immediately. Send your complete new address to Ornithological Societies of North America, % Sandra L. L. Gaunt, Box 21160, Columbus, Ohio 43221.

The permanent mailing address of the Wilson Ornithological Society is: c/o The Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109. Persons having business with any of the officers may address them at their various addresses given on the back of the front cover, and all matters pertaining to the Bulletin should be sent directly to the Editor.

Membership Inquiries

Membership inquiries should be sent to Dr. Keith Bildstein, Department of Biology, Winthrop College, Rock Hill, South Carolina 29733.

This issue of *The Wilson Bulletin* was published on 22 April 1982.

CONTENTS

THE STATUS OF THE AVIFAUNA OF THE REVILLAGIGEDO ISLANDS, MEXICO
Joseph R. Jehl, Jr., and Kenneth C. Parkes 1

AVIAN POPULATION FLUCTUATIONS DURING DROUGHT CONDITIONS IN PUERTO RICO
John Faaborg 20

NEST-SITES AND HABITAT OF RED-SHOULDERED AND RED-TAILED HAWKS IN IOWA
James C. Bednarz and James J. Dinsmore 31

BREEDING BIOLOGY AND DIET OF THE FERRUGINOUS HAWK IN SOUTH DAKOTA
Charles L. Blair and Frank Schitoskey, Jr. 46

IMPLICATIONS OF CONSTRUCTION OF A FLOOD CONTROL PROJECT UPON BALD EAGLE NESTING ACTIVITY ---------- *Anne E. Shapiro, Frank Montalbano, III, and Doris Mager* 55

FUNGI AND RED-COCKADED WOODPECKER CAVITY TREES
Richard N. Conner and Brian A. Locke 64

GENERAL NOTES

THE HUMEROULNAR PULLEY AND ITS EVOLUTION IN HUMMINGBIRDS
Gregory D. Bentz and Richard L. Zusi 71

RELATIONSHIPS OF ENVIRONMENTAL FACTORS TO ONSET OF AUTUMN MORNING VOCALIZATIONS IN AN OZARK COMMUNITY -------- *Richard M. Zammuto and Douglas James* 74

POSSIBLE COURTSHIP BEHAVIOR BY SNOWY OWLS IN WINTER
Peter C. Boxall and M. Ross Lein 79

DIFFERENTIAL HUNTING SUCCESS IN A GROUP OF SHORT-EARED OWLS
Thomas G. Marr and Douglas W. McWhirter 82

OBSERVATIONS AT A LAUGHING FALCON NEST *Mark B. Robbins and David A. Wiedenfeld* 83

EVIDENCE OF BALD EAGLES FEEDING ON FRESHWATER MUSSELS
Teryl G. Grubb and Michael A. Coffey 84

KILLDEERS FEEDING ON FROGS ---------- *Bette J. Schardien and Jerome A. Jackson* 85

POSSIBLE USE OF LEGS AS DISSIPATORS OF HEAT IN FLYING CLIFF SWALLOWS
Robert W. Butler 87

ACTIVE ANTING BY THE YELLOW-SHOULDERED BLACKBIRD
William Post and Micou M. Browne 89

COMPETITION BETWEEN RED-WINGED BLACKBIRDS AND COMMON GRACKLES
Sarah Lenington and Rose Scola 90

INCIDENCE OF BROWN-HEADED COWBIRD PARASITISM ON RED-WINGED BLACKBIRDS
George M. Linz and Susan B. Bolin 93

WESTERN KINGBIRD NESTS IN ABANDONED WOODPECKER CAVITY -- *Benedict C. Pinkowski* 95

PIRACY BY A GREAT BLACK-BACKED GULL ON A SHARK ---------- *Thomas W. French* 96

ORNITHOLOGICAL LITERATURE ---------- 97

ORNITHOLOGICAL NEWS ---------- 104

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 94, NO. 2 JUNE 1982 PAGES 105–240

THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

President—Abbot S. Gaunt, Department of Zoology, Ohio State University, Columbus, Ohio 43210.

First Vice-President—Jerome A. Jackson, Department of Biological Sciences, P.O. Drawer Z, Mississippi State University, Mississippi State, Mississippi 39762.

Second Vice-President—Clait E. Braun, Wildlife Research Center, 317 West Prospect St., Fort Collins, Colorado 80526

Editor—Jon C. Barlow, Department of Ornithology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6.

Secretary—Curtis S. Adkisson, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.

Treasurer—Robert D. Burns, Department of Biology, Kenyon College, Gambier, Ohio 43022.

Elected Council Members—Richard C. Banks (term expires 1982); Mary H. Clench (term expires 1983); Helen Lapham (term expires 1984).

Membership dues per calendar year are: Active, $16.00; Student, $14.00; Sustaining, $25.00; Life memberships $250 (payable in four installments).

THE WILSON BULLETIN is sent to all members not in arrears for dues.

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Now two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution, thus making available to all Society members the more important new books on ornithology and related subjects. The fund will be administered by the Library Committee, which will be happy to receive suggestions on the choice of new books to be added to the Library. William A. Lunk, University Museums, University of Michigan, is Chairman of the Committee. The Library currently receives 195 periodicals as gifts and in exchange for *The Wilson Bulletin*. With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to: The Josselyn Van Tyne Memorial Library, University of Michigan Museum of Zoology, Ann Arbor, Michigan 48109. Contributions to the New Book Fund should be sent to the Treasurer (small sums in stamps are acceptable). A complete index of the Library's holdings was printed in the September 1952 issue of *The Wilson Bulletin* and newly acquired books are listed periodically. A list of currently received periodicals was published in the December 1978 issue.

THE WILSON BULLETIN
(ISSN 0043-5643)

The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September, and December. The subscription price, both in the United States and elsewhere, is $20.00 per year. Single copies, $4.00. Subscriptions, changes of address and claims for undelivered copies should be sent to the OSNA, Box 21160, Columbus, Ohio 43221. Most back issues of the *Bulletin* are available and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Joselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan 48109. Known office of publication: Department of Zoology, Ohio State University, 1827 Neil Avenue, Columbus, Ohio 43210.

Second class postage paid at Columbus, Ohio and at additional mailing office.

© Copyright 1982 by the Wilson Ornithological Society

Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

MUS. COMP. ZOOL.
LIBRARY
JUL 6 1982
HARVARD
UNIVERSITY

Grallaria carrikeri (Pale-billed Antpitta), a new species from Peru.
Painting by John P. O'Neill

424

THE WILSON BULLETIN
A QUARTERLY MAGAZINE OF ORNITHOLOGY
Published by the Wilson Ornithological Society

VOL. 94, NO. 2 JUNE 1982 PAGES 105–240

Wilson Bull., 94(2), 1982, pp. 105–113

A NEW SPECIES OF ANTPITTA (*GRALLARIA*) FROM NORTHERN PERU

THOMAS S. SCHULENBERG AND MORRIS D. WILLIAMS

Antbirds (Formicariidae) have a well-deserved reputation as shy, secretive birds. These attributes apply in particular to the poorly-known antpittas (*Grallaria* and allies). Although the cordilleras of the Eastern Andes of Peru have been a rich source of undescribed avian species, we were nonetheless surprised to encounter a distinctly different antpitta in 1978 during faunal surveys for the Louisiana State University Museum of Zoology (LSUMZ) in the Department of Amazonas, northern Peru. Additional specimens of this bird were obtained during further LSUMZ fieldwork in 1979 in the Department of La Libertad, Peru. This antpitta represents an undescribed species that we propose to call:

Grallaria carrikeri sp. nov.

PALE-BILLED ANTPITTA

HOLOTYPE.—Louisiana State University Museum of Zoology No. 88044; adult male from Cordillera Colán, SE La Peca, ca. 5°34′S, 78°19′W, 2450 m, Dept. Amazonas, Peru; 15 October 1978; collected by M. D. Williams; original number 2056.

DIAGNOSIS.—A medium-sized antpitta that most closely resembles *Grallaria nuchalis* (especially the nominate subspecies) in size and general color of the back, wings and underparts. Distinguished from all populations of *G. nuchalis* by the black face and throat, by the absence of rust on the nape, by the narrow black tips to the feathers of the back and breast, by the red iris, and by the strikingly pale, whitish bill, which appears to be unique in the family.

DISTRIBUTION.—Known from three localities in the Eastern Andes of northern Peru (see Fig. 1): Cordillera Colán, SE La Peca, ca. 5°34′S, 78°19′W, 2350–2550 m, Dept. Amazonas; 33 road km NE Ingenio on road to Laguna Pomacochas, ca. 5°52′S, 77°57′W, 2550 m, Dept. Amazonas; and Cumpang, above Utcubamba, on trail to Ongón, ca. 8°12′S, 77°10′W, 2750–2900 m, Dept. La Libertad. Probably occurs more or less continuously along the east slope of the Eastern Andes south of the Río Marañón at least to Cumpang,

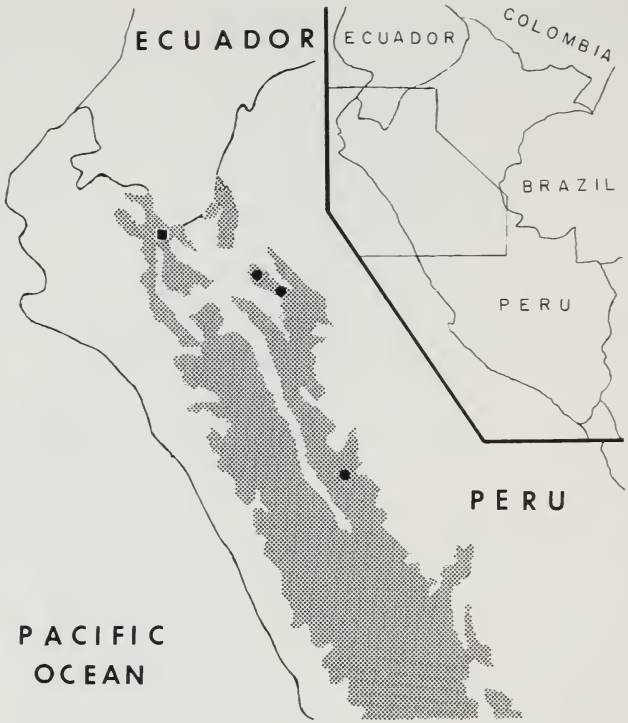


FIG. 1. The Andes of northwestern Peru (shaded within the 2000 m contour) showing the distribution in Peru of *Grallaria nuchalis* (square, upper left) and *G. carrikeri* (circles). Note that the two species are separated by the low, arid Río Marañón valley. The three localities for *G. carrikeri* are, from upper left to lower right: Cordillera Colán (type locality), northeast of Ingenio, and Cumpang.

and possibly farther south, as large areas of uninterrupted forest remain in this region at elevations inhabited by *G. carrikeri*.

DESCRIPTION OF THE HOLOTYPE.—Lores, forecrown, malar region and base of auriculars black; crown and tips of auriculars shading through blackish-brown to Claret Brown (capitalized color names are from Ridgway 1912) on nape. Back and rump Medal Bronze, feathers very narrowly tipped black. Remiges dusky-brown, outer webs of remiges Mahogany Red; upper wing coverts Mahogany Red. Rectrices dusky-brown. Chin black, shading to blackish-gray on throat. Underparts light gray, shading darker on sides of breast and paler posteriorly, to almost white in center of belly; feathers on breast and upper belly narrowly tipped black. Flanks and undertail coverts Buffy Citrine. Thigh feathers Mouse Gray. Soft-part colors in life: bill ivory; iris pale reddish brown; legs and feet blue-gray.

MEASUREMENTS OF HOLOTYPE.—Chord of wing 111.6 mm; tail 66 mm; culmen from base 30 mm; tarsus 59 mm; weight 111 g.

SPECIMENS EXAMINED.—*G. carrikeri*: Cordillera Colán, Peru, 4 ♂♂ (LSUMZ 88042–88045), 1 ♀ (LSUMZ 88046), 1 ♀ skeleton (LSUMZ 89957); NE Ingenio, Peru, 1 ♂

(DMNH 60082); Cumpang, Peru, 3 ♂♂ (LSUMZ 92456–92457, 92460), 3 ♀♀ (LSUMZ 92458–92459, 92461).

G. n. nuchalis: Cerro Chinguela, Peru, 2 ♂♂ (LSUMZ 88041, 97679), 2 ♀♀ (LSUMZ 97678, 97680); Oyacachi, Ecuador, 1 ♀ (AMNH 180253); Sumaco Arriba, Ecuador, 2 ♀♀ (AMNH 184379, 184381); Maspa, Ecuador, 1 ♂ (AMNH 173024); Baeza, Ecuador, 1 ♂ (AMNH 173023).

G. n. obsoleta: Verdecocha, Ecuador, 1 ♂ (AMNH 180254), 2 ♀♀ (AMNH 173304, 180255); Pichincha, Ecuador, 1 ♂ (AMNH 492198); below Mindo, Ecuador, 1 sex unknown (AMNH 156756).

G. n. ruficeps: Almaguer, Colombia, 2 ♂♂ (AMNH 116340, 116343), 2 ♀♀ (AMNH 116338–116339); Laguenta, Colombia, 2 ♂♂ (AMNH 111972, 111974), 1 ♀ (AMNH 111969); Cauca Valley, Colombia, 1 ♀ (AMNH 492197).

ETYMOLOGY.—We take pleasure in naming this species after the late M. A. Carriker, Jr., who, over a lifetime of fieldwork in South America, contributed enormously to the knowledge of Andean birds. It is particularly fitting to name this species in Carriker's honor, as he collected in both Amazonas and La Libertad, near the areas where the new species was discovered.

REMARKS

Variation in the type series.—Males average slightly larger than females (Table 1). There is only slight paratypic variation in plumage color, which does not appear to be related to sex. Variation is most evident in the color of the underparts; some individuals are darker gray on the breast than the holotype. The centers of the upper breast feathers of one female (LSUMZ 92461) are brown; other females do not exhibit this feature. Five specimens have from 1–3 white feathers on the head and nape. We have not detected a similarly high frequency for this minor plumage aberration in other species of antpitta. Descriptions of soft-part colors (as noted on specimen labels) vary somewhat. Descriptions of bill color vary from "ivory" (holotype) and "white" to "very pale yellow-green, base shaded light blue." Descriptions of iris color vary from "light brown" through "pale creamy-orange" to "crimson red." These differences may be due in part to rapid post-mortem changes in iris color; irides that are red immediately after death soon begin to pale and turn brown.

Juvenal plumage.—D. G. Wysham collected a juvenile antpitta (DMNH 60082) northeast of Ingenio on 9 August 1976. Originally identified as a Chestnut-naped Antpitta (*G. nuchalis*), this specimen (the only one from this locality) is undoubtedly *G. carrikeri*. The bird weighed 90 g. Remiges are fully developed (wing chord 104 mm), although the rectrices are not fully grown. The head is blackish-gray with black lores. Feathers on the nape are tinged brown and tipped with cinnamon. Most of the rest of the body is brown, barred with black; barring becomes obsolete on the lower belly. The shade of brown varies from Auburn on the upper back to cinnamon-buff on the lower back and breast. The belly is buffy with a creamy-

Table 1

Measurements of *Grallaria nuchalis* and *G. carrikeri*

Measurements	*G. n. ruficeps*			*G. n. obsoleta*			*G. n. nuchalis*			*G. carrikeri*		
	N	$\bar{x}$	Range	N	$\bar{x}$	Range	N	$\bar{x}$	Range	N	$\bar{x}$	Range
Wing (chord) (mm)	4 ♂♂	115.4	113.8–120.3	2 ♂♂	111.9	110.4–113.4	4 ♂♂	107.2	99.6–112.7	5 ♂♂	110.1	106.8–112.5
	4 ♀♀	117.7	116.0–118.6	2 ♀♀	109.9	108.9–110.9	5 ♀♀	105.5	100.8–109.9	2 ♀♀	105.4	103.7–107.1
				1 unk.	109.9							
Tail (mm)	3 ♂♂	67.5	65.7–70.7	2 ♂♂	63.0	60.1–65.8	3 ♂♂	64.2	59.8–67.7	4 ♂♂	64.6	62.6–66.0
	3 ♀♀	67.9	65.7–70.4	2 ♀♀	61.7	61.6–61.7	4 ♀♀	61.4	57.5–67.0	4 ♀♀	63.4	61.4–65.7
				1 unk.	57.8							
Culmen from base	2 ♂♂	31.4	—	2 ♂♂	27.8	27.7–27.9	3 ♂♂	28.9	25.9–30.8	5 ♂♂	30.1	29.6–31.3
(mm)	3 ♀♀	30.0	29.0–30.9	2 ♀♀	27.4	27.1–27.6	5 ♀♀	28.9	27.0–31.2	4 ♀♀	28.4	28.0–29.1
				1 unk.	27.7							
Tarsus (mm)	3 ♂♂	57.4	55.0–59.0	2 ♂♂	57.3	56.7–57.9	3 ♂♂	53.4	48.8–59.3	5 ♂♂	59.7	59.0–60.6
	4 ♀♀	59.4	57.3–60.9	2 ♀♀	53.7	52.9–54.4	5 ♀♀	54.3	51.2–57.4	4 ♀♀	57.7	56.4–58.9
				1 unk.	51.8							
Weight (g)	—	—	—	—	—	—	2 ♂♂	119	115–122	5 ♂♂	112	96–124
							2 ♀♀	116	110.0–122	5 ♀♀	107	97–112

white area in the center. There are a few gray feathers on the side of the breast. The primary wing coverts are tipped cinnamon-buff, with a black subterminal band. The iris color was not described; the bill was described as "orange flecked with black, basally orange"; the tarsi were "gray-flesh, scute edges darker."

A specimen (LSUMZ 88042; skull 40% ossified; 86 g; irides brownish-red; maxilla blackish, tomia salmon; distal culmen whitish; mandible dusky, base and tomia salmon; tarsi blue-gray) collected 21 October 1978 at the type locality shows about an equal mixture of juvenal and definitive plumage. The crown, nape, and wing coverts are entirely juvenal, and juvenal feathers are scattered throughout the back, rump, breast and belly. Another specimen (LSUMZ 88043; skull 50% ossified; 97.5 g; soft-part colors similar to the last specimen) collected at the same locality on 19 October 1978, retains juvenal wing coverts, the juvenal crown and nape feathers and two juvenal breast feathers. Two additional specimens from this locality, both with fully ossified skulls and adult bill color, retain juvenal wing coverts, but otherwise exhibit typical definitive plumage.

Breeding and molt.—Juvenile *G. carrikeri* were collected in August 1976 and October 1978 in Dept. Amazonas, suggesting that the species breeds primarily during the drier part of the year. A nest with recently-hatched young, however, was discovered at Cumpang in October 1979 (Wiedenfeld, in press). Three adult females collected at Cumpang in October did not show enlarged follicles, brood patches, or other evidence of breeding. Likewise, testes of adult males collected in October are only slightly enlarged (largest 7 × 3 mm). Half of the adult specimens show light to moderate body molt. Light tail molt is apparent on three specimens, and one specimen is molting two primaries.

Habitat and ecology.—All three localities from which the new species is known are in cloud forest. At these localities the forest is up to 30 m tall, the canopy is broken and epiphytic growth is lush. Forest undergrowth is typically dense, and bamboo often forms large thickets. *G. carrikeri* were often noted in or near such bamboo thickets, usually on or within a meter of the ground.

The elevational distribution of *G. carrikeri* overlaps the lower elevational limits of two sympatric species of *Grallaria*: Undulated Antpitta (*G. squamigera*) and Rufous Antpitta (*G. rufula*), and overlaps the upper elevational limits of yet two more species: Chestnut-crowned Antpitta (*G. ruficapilla*) and Rusty-tinged Antpitta (*G. przewalskii*). At each locality where *G. carrikeri* is known, it is syntopic with two or three of these species: *G. squamigera* (Cumpang, $\bar{x}$ = 144.3 g, N = 4); *G. ruficapilla* (northeast of Ingenio, $\bar{x}$ = 88 g, N = 2); *G. przewalskii* (Cordillera Colán, northeast of Ingenio, Cumpang; $\bar{x}$ = 68.5 g, N = 13); *G. rufula* (Cordillera

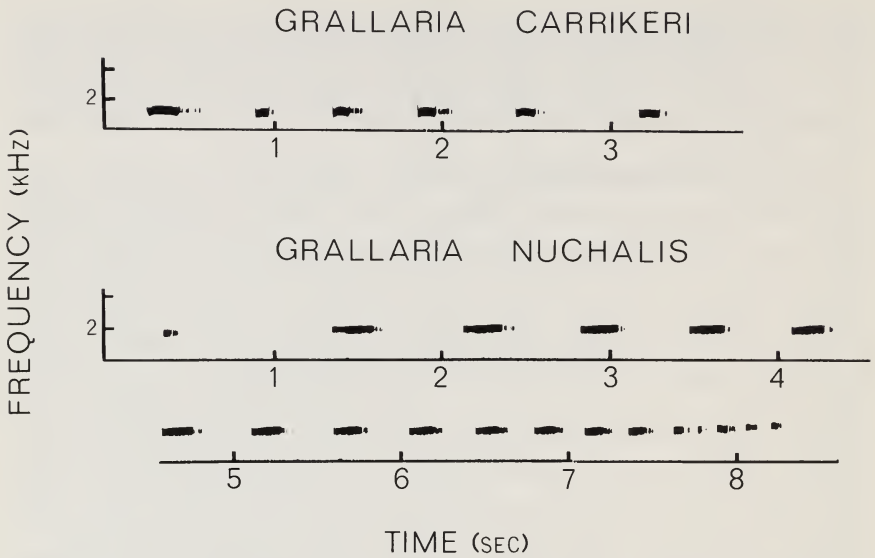


FIG. 2. Songs of *Grallaria carrikeri* (Cumpang, Dept. La Libertad, Peru) and *G. nuchalis* (Cerro Chinguela, Dept. Cajamarca, Peru). The two species differ in the length and pattern of the song. Both species recorded by T. A. Parker, III.

Colán, Cumpang; $\bar{x}$ = 41.6 g, N = 15). Little is known yet about possible microhabitat segregation or other ecological differences among these species. Stomachs of seven *G. carrikeri* were examined and contained arthropods, especially caterpillars (in four stomachs, lengths 12–34 mm), and beetles (in four stomachs). Qualitatively similar food items have been identified in stomachs of *G. squamigera*, *G. nuchalis*, *G. przewalskii* and *G. rufula* (specimen tag data, LSUMZ).

Voice.—Tape recordings and sonograms of the songs of *G. n. nuchalis* and *G. carrikeri* were made available to us by T. A. Parker, III, who recorded both species in Peru (tapes deposited at the Library of Natural Sounds, Cornell University Laboratory of Ornithology). Songs of both species are shown in Fig. 2. The song of *G. carrikeri* contains six notes. The spacing between the notes is not even, as there are slight pauses between the first and second, and fifth and sixth notes. The song is 3 sec long. The song of *G. nuchalis* is longer (ca. 8 sec), and consists of a gradually accelerating series of notes. The individual notes of the songs of both species are structurally similar, but the songs are quite different in the pattern of notes. The song of *G. nuchalis* is about 0.5 kHz higher in pitch than is the song of *G. carrikeri*. The songs of the two species also

differ qualitatively; the song of *G. carrikeri* sounds staccato, while the song of *G. nuchalis* has a ringing quality.

Songs of these two species are sufficiently different to suggest that they could function as a reproductive isolating mechanism. Support for this hypothesis comes from playback experiments on *G. nuchalis* conducted by Parker and M. J. Braun in June and July 1980 at Cerro Chinguela, 2800 m, Dept. Cajamarca, Peru. In a series of trials, tapes of *G. carrikeri* recorded at Cumpang elicited no response from *G. nuchalis*. These same *G. nuchalis* responded to playbacks of *G. nuchalis* songs by approaching the experimenters, sometimes hopping into the open, and singing. The initial vocalization of some *G. nuchalis* responding to playback tapes was a high-pitched *chee-chee-chee-chee-chee* (Parker, pers. comm.). This type of vocalization is not known from *G. carrikeri*. Unfortunately, reciprocal playbacks (testing *G. carrikeri* with *G. nuchalis* tapes) have not been performed.

Systematic relationships.—Morphologically *G. carrikeri* bears a close resemblance to *G. nuchalis* (see Table 1), which occurs at similar elevations from Colombia to northern Peru. Differences in plumage and soft-part colors (see Diagnosis) and song (above) suggest that *G. carrikeri* has achieved species status. These two species are completely isolated from one another by an area of unsuitable habitat formed by the arid Río Marañón valley. Several other probable allospecies pairs, which differ on the basis of plumage characters to about the same degree as these two antpittas, are also separated by this Marañón discontinuity, e.g., Neblina Metaltail (*Metallura odomae*)/Coppery Metaltail (*M. theresiae*) (see Graves 1980), Flammulated Treehunter (*Thripadectes flammulatus*)/Buff-throated Treehunter (*T. scrutator*), and Black-headed Hemispingus (*Hemispingus verticalis*)/Drab Hemispingus (*H. xanthophthalmus*).

On the basis of either voice or plumage characters, *G. nuchalis* and *G. carrikeri* do not appear to be particularly closely allied to any other members of the genus. Zimmer (1934) considered *G. nuchalis* to have a "definite relationship" to the White-throated Antpitta (*G. albigula*) of southeastern Peru and Bolivia on the basis of shared similarities in coloration and structure. We tend to agree more with Chapman (1923), who described *G. albigula*, that the details of coloration of *G. albigula* show greater resemblance to *G. ruficapilla* (dorsally) and *G. hypoleuca* (ventrally), and we see no particular plumage similarities to *G. nuchalis*. Zimmer (1934) noted that *G. albigula* did not share the stout, strongly decurved bill of *G. nuchalis* [and *G. carrikeri*], but apparently did not assign much importance to this feature; we would interpret this difference as further evidence that *G. albigula* is not closely related to *G. nuchalis* and *G. carrikeri*. The

song of *G. albigula* is a mellow, whistled *hoo-hoo*, with the second syllable higher in pitch than the first. This song bears similarities to the songs of *G. ruficapilla* and *G. przewalskii*, but is completely unlike the songs of *G. nuchalis* and *G. carrikeri*.

As noted above, the distribution of *G. carrikeri* is limited to the north by the Río Marañón valley. Surprisingly, *G. carrikeri* has not been found in the now comparatively well-known Cordillera Carpish in Dept. Huánuco, only 180 km south of Cumpang, despite the presumed availability of suitable habitat in the intervening areas. The same distributional pattern (southern Dept. Amazonas south to Dept. La Libertad, but not to Dept. Huánuco) is shared in whole or in part by at least one mammal, the yellow-tailed woolly monkey (*Lagothrix flavicauda*) (Parker and Barkley 1981) and several other birds: Yellow-browed Toucanet (*Aulacorhynchus huallagae*), Russet-mantled Softtail (*Thripophaga berlepschi*), Rusty-tinged Antpitta (*Grallaria przewalskii*), Tawny Antpitta (*G. quitensis atuensis*) and Crowned Chat-Tyrant (*Ochthoeca frontalis orientalis*). We do not know what factors, historical or ecological, determine the southern limit of distribution of *G. carrikeri*. We believe, however, that the distribution of this species, and of the other taxa mentioned above, suggests that a Pleistocene refuge of montane forest may have existed somewhere in what is now Dept. Amazonas, Dept. San Martín, or Dept. La Libertad.

ACKNOWLEDGMENTS

Many people worked very hard under strenuous field conditions during the expeditions that obtained the new species. In particular we acknowledge contributions by P. J. Barbour, L. J. Barkley, P. L. Brown, J. W. Eley, G. L. Graham, T. A. Parker, III, M. B. Robbins, D. A. Wiedenfeld, and our perennial and indispensable field assistants, Reyes Rivera A., Manuel Sánchez S. and Klaus Wehr. Arturo and Helen Koenig, Manuel and Isabel Plenge, and Gustavo del Solar R. helped make us feel at home in their country, and provided logistical support for our operations. We appreciate the valuable criticisms of the manuscript by E. Eisenmann, G. R. Graves, T. A. Parker, III, K. C. Parkes and J. V. Remsen, Jr. We are especially grateful to T. A. Parker, III, for permission to use his tapes and notes on the new species, and to J. P. O'Neill for the color plate. Sonograms were prepared by J. L. Gulledge of the Cornell University Laboratory of Ornithology. D. M. Niles, Delaware Museum of Natural History (DMNH), and W. E. Lanyon, American Museum of Natural History (AMNH) loaned comparative material. Ing. Eric Cardich Briceño and his staff of the Dirección General Forestal y de Fauna of the Ministerio de Agricultura, Lima, Peru, continue their support of the LSUMZ field studies. We are most grateful to John S. McIlhenny, H. Irving and Laura R. Schweppe and Babette M. Odom for their continued interest in and support of the LSUMZ fieldwork. Comparative studies of antpittas at the American Museum of Natural History were aided by grants to the authors from the Frank M. Chapman Memorial Fund in 1979.

We dedicate this paper to the late Eugene Eisenmann in recognition of his many contributions to neotropical ornithology.

LITERATURE CITED

CHAPMAN, F. M. 1923. Descriptions of proposed new Formicariidae and Dendrocolaptidae. Am. Mus. Novit. 86:1–20.

GRAVES, G. R. 1980. A new species of metaltail hummingbird from northern Peru. Wilson Bull. 92:1–7.

PARKER, T. A., III, AND L. J. BARKLEY. 1981. New locality for the Yellow-tailed Woolly Monkey. Oryx 16:71–72.

RIDGWAY, R. 1912. Color standards and color nomenclature. Washington, D.C. (Published by the author.)

WIEDENFELD, D. In press. A nest of the Pale-billed Antpitta (*Grallaria carrikeri*) with comparative remarks on the nests of antpitta species. Wilson Bull.

ZIMMER, J. T. 1934. Studies of Peruvian birds. XII. Notes on *Hylophylax*, *Myrmothera*, and *Grallaria*. Am. Mus. Novit. 703:1–21.

MUSEUM OF ZOOLOGY, LOUISIANA STATE UNIV., BATON ROUGE, LOUISIANA 70893. ACCEPTED 23 OCT. 1981.

COLORPLATE

The colorplate Frontispiece of Pale-billed Antpitta (*Grallaria carrikeri*) has been made possible by an endowment established by George Miksch Sutton.

Wilson Bull., 94(2), 1982, pp. 114–128

THE RELATIONSHIPS OF THE VIREOS (VIREONINAE) AS INDICATED BY DNA-DNA HYBRIDIZATION

Charles G. Sibley and Jon E. Ahlquist

The New World passerine subfamily Vireoninae contains 43 species in four genera. *Vireo*, the largest genus, is primarily North American but several of its 25 species occur on Caribbean islands, one species has a subspecies in Bermuda, and two species occur as far south as Argentina. The 13 species of Neotropical greenlets (*Hylophilus*) are primarily South American; three occur in Central America of which one reaches southern Mexico. *Vireo* and *Hylophilus* are the "typical" vireos, being relatively small passerines with green, yellow and gray plumage colors. The other two genera, *Vireolanius* and *Cyclarhis*, are larger, brighter in color, and with heavy, shrike-like bills. The three species of shrike-vireos (*Vireolanius*) occur from southern Mexico to Bolivia, and the two species of pepershrikes (*Cyclarhis*) range from southern Mexico to Uruguay (Thomson 1964, Blake 1968).

Opinions about the relationships of the vireos to other oscine passerines (Passeres) have focused primarily upon two groups, namely: the shrikes (Laniidae), and the New World nine-primaried oscines, particularly the wood warblers (Parulini of Sibley 1970; Sibley and Ahlquist 1982b).

The vireos have been thought to be related to the shrikes because they have a shrike-like bill with a hooked tip and a subterminal notch in the maxillary tomium (e.g., Coues 1892). The principal basis for placing the vireos near the nine-primaried oscines has been the size and coloration of the typical vireos and their tendency toward the reduction of the outer (10th) primary (e.g., Mayr and Amadon 1951:27).

In this paper, we present data from quantitative comparisons of the single-copy DNA sequences showing that the vireos, greenlets, pepper-shrikes and shrike-vireos are closely related to one another, and that they are not closely related to the New World nine-primaried oscines, but are members of a large "corvine" assemblage that includes the corvids (Corvidae), shrikes (Laniidae), drongos (*Dicrurus*), monarchs (*Monarcha*), cuckoo-shrikes (Campephagidae) and several other groups. The following review of the taxonomic history of the vireos demonstrates the difficulties and controversies involved in the discovery and interpretation of the traditional characters that have been used as the basis for opinions about the relationships among birds in general, and the vireos in particular.

TAXONOMIC HISTORY OF THE VIREOS

Baird (1858) first included the Vireoninae in the Laniidae, because of the "same abrupt and lengthened hook" at the tip of the bill, but by 1864 he had placed the vireos in a separate family, Vireonidae. Sclater and Salvin (1873) agreed with Baird (1864) but Sundevall (1872) placed *Hylophilus* and *Cyclarhis* (plus *Dulus*) in the "Fam. Hylophilinae," and *Vireo* in the "Fam. Vireoninae."

To Parker (1878:282–284) the skull of *Cyclarhis* was so similar to that of "*Suthora bulomachus*" (=*Paradoxornis webbianus*, Webb's Parrotbill) of China that he despaired of discovering "the laws of the geographical distribution of birds." Parker considered *Paradoxornis* to be a parid and dubbed *Cyclarhis* "this large archaic Tit," but he left *Cyclarhis* in the Vireonidae. *Paradoxornis* was placed in the Panurinae of the Timaliidae by Deignan (1964).

Gadow (1883) included the vireos as a subfamily of his Laniidae primarily because of the bill characters. Other subfamilies in Gadow's Laniidae were the Gymnorhininae, which included the Australian magpies and butcherbirds (Cracticidae) and the Bornean Bristlehead (*Pityriasis gymnocephala*). The vanga shrikes (Vangidae) of Madagascar, and some of the African and southeast Asian shrikes, were placed in the Malaconotinae. Gadow's (1883) Pachycephalinae included the Australo-Papuan genera *Falcunculus*, *Oreoica*, *Eopsaltria*, *Pachycare* and *Pachycephala*. These may seem like strange companions for the New World vireos, but, as will become apparent, Gadow was closer to the mark than the many later taxonomists who allied the vireos to the wood warblers. (See Sibley and Ahlquist 1982b.)

Coues (1892:329) considered the vireos to be "small dentirostral *Oscines*, related to the Shrikes, with hooked bill, 10 primaries and extensively coherent toes." Coues placed the vireos in their own family, next to the Laniidae, and he commented (1892:331): "But that the important character of number of primaries—one marking whole families . . . should here subside to specific value only, seemed suspicious; and the fact is that all the species really have 10, only that, in some instances, the 1st primary is rudimentary and displaced, lying concealed outside the base of the second quill."

Ridgway (1904:233) placed the Vireonidae next to the Laniidae but expressed "great doubt whether the . . . groups comprising Dr. Gadow's Laniidae . . . can, any of them, be properly included in the same family . . ." with the true shrikes.

Pycraft (1907:375) noted that the Vireonidae were thought by some to be related to the Sylviidae, by others to the Laniidae but, in his opinion

(which was based upon skeletal comparisons) only *Cyclarhis* is a shrike, *Vireolanius* is related to the Artamidae, and *Vireo* to the Muscicapidae.

Naumburg (1925) observed that "the bill of *Cyclarhis* . . . is very similar to that of *Falcunculus* [of the Pachycephalidae of the Australian region] which it also resembles so much in other characters as usually to induce authors to bring the two together either as adjacent genera or as belonging to closely allied sub-families."

Wetmore (1930) took "the work of Hans Gadow" as his starting point and incorporated such changes "as seem justified from personal research or from the investigations of others." This led Wetmore to place the Cyclarhidae and Vireolaniidae near the shrikes, but to dissociate the typical vireos from them and to place his Vireonidae between the nine-primaried Old World white-eyes (Zosteropidae) and the Neotropical nine-primaried honeycreepers (Coerebidae), and close to the other New World nine-primaried oscines, including the wood warblers. This arrangement seems to have been based, in part, upon Pycraft's (1907) claim that only *Cyclarhis* is a shrike and that *Vireolanius* is related to *Artamus*. This is indicated by Wetmore's (1951:11) opposition to the opinion of Zimmer (1942:10), who had expressed his belief that *Cyclarhis* and *Vireolanius* should not "be given family distinction from the Vireonidae. They are heavy-billed, heavy-footed vireos, with a vireonine pattern of coloration . . . and vireonine habits . . . . I should be loath to place a subfamily Vireolaniinae in the family Artamidae" as suggested by Pycraft (1907).

In reply, Wetmore (1951:11, 1960:20) argued that "while Zimmer [1942] believes that the family Vireolaniidae should be included in the Vireonidae, separate family rank in my opinion is definitely justified. In addition to the characters assigned by Pycraft for the shrike-vireos, I have found recently that in the pterylosis the dorsal tract . . . is forked, the arms . . . broad . . . separated from the . . . line . . . onto the caudal area. This is . . . different from the usual rhomboid found in the vireos, and may indicate that the family eventually should be removed from the vicinity of the Vireonidae." Wetmore (1951) also referred to the skeletal characters "outlined by Pycraft [1907]" to support his family distinction for the Cyclarhidae. Wetmore used the same arrangement of three separate families in the last edition (1960) of his classification.

Wetmore's (1951, 1960) association of the typical vireos with the New World nine-primaried assemblage apparently was dictated by his belief in their distinctness from the shrike-vireos and peppershrikes, coupled with the tendency for the reduction of the 10th primary in *Vireo*.

Hellmayr (1935) used a relatively neutral sequence of families: Vireonidae, Vireolaniidae, Cyclarhidae, Laniidae, Sturnidae, Coerebidae and Compsothlypidae (=Parulidae). Mayr and Amadon (1951:21) viewed the

shrike-like bill of the vireonids as due to convergence and placed the Vireonidae (including *Vireolanius* and *Cyclarhis*) in their "Vireos, Finches, and Allies" which included the New World nine-primaried groups.

From his study of jaw muscles and other anatomical characters Beecher (1953) developed an intriguing combination of the shrike and wood warbler theories of the relationships of the vireos. He wrote (1953:273) that "judging from anatomical and other characters, the . . . vireos . . . are apparently descendants of the Old World insect-eaters that were cut off when the northern exchange corridor submerged or became too cold. Subsequently, the vireos gave rise to the entire nine-primaried American assemblage. They appear directly ancestral to the . . . tanagers and . . . warblers . . . the Oscines existed only as insect-eaters when the Vireonidae became isolated in the New World, and . . . this happened *before* the origin of the flowering plants or about the same time." Beecher (1953:294) included the vireos with the monarchs, whistlers (*Pachycephala*) and drongos in the family Monarchidae, characterized by "a winged ectethmoid, [with] a large single foramen, a fused lacrymal . . . a prominent postorbital process . . . [and] specialized bills . . . ." Beecher (1953:324) placed his Monarchidae next to "The American Nine-Primaried Assemblage" and concluded that "it seems particularly clear that the American nine-primaried families arose from the vireos (Vireoninae), a subfamily of the Monarchidae" (Beecher 1953:305).

Beecher's (1953:324) phylogenetic tree splits the oscines into two "superfamilies," Sylvioidea and Timalioidea. We have found that the prototypes of these two groups, the sylviine warblers and timaliine babblers, are actually ecotypes of a monophyletic cluster, so closely related that we have felt obliged to include both groups in the Sylviidae (Sibley and Ahlquist 1982c).

Thus, although much of Beecher's (1953) oscine phylogeny is untenable, he did find evidence of relationship between the vireos and the monarchines, with which we agree. His attempt to derive the American nine-primaried assemblage from the vireos may have been conditioned by Wetmore's influence.

Tordoff (1954a:7), "largely on the basis of studies by other authors," included the Vireonidae as the first family in the sequence of "Vireos, finches, and allies" (1954a:32). Tordoff (1954b) criticized Beecher (1953) for thinking "that the Vireonidae . . . have existed *as vireos* in the New World since some time in the Cretaceous" and identified the "Fringillidae" (by which he meant the cardinals, the tanagers, and the genus *Fringilla*) to be "the central stock" of the New World nine-primaried oscines, while the vireos "are shown to be derivable from primitive finches . . . ." (1954b:283).

Stallcup (1954) reported that certain features of the leg musculature of *Vireo* agree better with the condition in the cardinalines, emberizines, tanagers, wood warblers and icterines, than with that in the carduelines and ploceids. However, in a serological study, Stallcup (1961) found that *Vireo* is not particularly close to the tanagers (*Piranga*) or to the cardinalines (*Cardinalis*). In fact, *Vireo* was not close to any of the other oscines with which it was compared, including *Lanius*.

Bock (1960:471) considered the vireos to be "the most likely representatives of the ancestral nine-primaried stock" but, after listing the anatomical characters upon which he based this opinion, he concluded (1960:472) that "this evidence is not very conclusive and much more is needed to verify this hypothesis."

Bock (1962) found that the vireos exhibit only the beginnings of a second fossa in the head of the humerus. The shrikes have a single fossa and in the American nine-primaried groups the fossa is double.

Sibley (1970) reviewed the evidence and concluded that "there is general agreement . . . that the vireos are probably allied to the New World nine-primaried oscines, but not as closely as the members of the latter group are to one another." Sibley interpreted the electrophoretic patterns of the egg-white proteins as supporting this position.

Barlow and James (1975) studied the behavior and nesting of the Chestnut-sided Shrike-Vireo (*Vireolanius melitophrys*) and concluded that the shrike-vireos should be included in the Vireonidae.

Raikow (1978) compared the appendicular musculature of the New World nine-primaried oscines and the vireos. He (1978:41) concluded that the Vireonidae, including *Cyclarhis* and *Vireolanius*, are not closely related to the nine-primaried assemblage, but that their position "remains problematical because their affinities are still obscure."

Orenstein and Barlow (1981:36) concluded that the variations in jaw musculature which they observed in the Vireonidae "seemed related to differences in foraging technique . . . and of little use in determining intrageneric relationships." The jaw muscle variants were correlated with certain groupings within *Vireo* "but their chief importance . . . has been as indicators of the range and kind of morphological variation that has occurred in the Vireonidae as a whole" (1981:36). Orenstein and Barlow (1981) also recommended the inclusion of *Cyclarhis* and *Vireolanius* in the Vireonidae.

The reduction of the outer primary in the vireos is correlated with the extent of migration, as demonstrated by Averill (1925) and Hamilton (1958, 1962). In species with the longest migrations the outer primary is reduced the most, producing a longer, more pointed wing. Stegmann (1962) also found a correlation between the reduction of the outer primary and strong

flight. Conversely, sedentary species, especially those living in dense vegetation, tend to evolve rounded wings with long outer primaries.

METHODS

To examine the taxonomic relationships between the genus *Vireo* and other passerines we have used the technique of DNA-DNA hybridization. Our procedures were based primarily upon those of Britten and Kohne (1968), Kohne (1970), and Britten et al. (1974). In our study of the ratite birds (Sibley and Ahlquist 1981a), we have described the technique in moderate detail, including a more extensive review of the relevant literature. The following is a synopsis of the methods used in the present study.

The genetic material, deoxyribonucleic acid (DNA), is a double-stranded molecule composed of linear sequences of four types of subunits (nucleotides) which differ in the chemical structures of their nitrogenous "bases," namely, adenine (A), thymine (T), guanine (G) and cytosine (C). In double-stranded DNA the bases occur as complementary pairs: an A in one strand pairs only with a T in the other strand, a G pairs only with a C. Genetic information is encoded in the sequences of the bases. The two strands of native DNA molecules will separate if heated in solution to ca. 100°C which ruptures ("melts") the hydrogen bonds between base pairs. Upon cooling, the double-stranded molecule re-forms because the complementary bases "recognize" one another and reassociate. If the temperature is maintained at or near 60°C base pairing will occur only between long homologous sequences of nucleotides. This is because only long sequences of complementary bases have sufficient bonding strength to maintain stable duplexes at that temperature, and only homologous sequences possess the necessary degree of complementarity. Thus, under appropriate conditions of temperature and salt concentration, the dissociated single strands of conspecific DNA will reassociate only with their homologous partners and the matching of complementary base pairs will be essentially perfect.

Similarly, if the single-stranded DNAs of two different species are combined under conditions favoring reassociation, "hybrid" double-stranded molecules will form between homologous sequences. These hybrid molecules will contain mismatched base pairs because of the nucleotide sequence differences (i.e., nucleotide substitutions) that have evolved since the two species diverged from their most recent common ancestor. The lower bonding strength of such hybrid molecules will cause them to dissociate at a temperature lower than that required to melt conspecific double-stranded DNA molecules. The reassociation of homologous sequences and the decreased thermal stability of imperfectly base-paired hybrid sequences form the basis of the DNA-DNA hybridization technique.

The extent of base-pair matching between the homologous nucleotide sequences of any two DNAs can be determined by measuring (1) the percentage of hybridization and (2) the thermal stability of the reassociated double-stranded molecules.

DNAs of the species in Table 1 were obtained from the nuclei of avian erythrocytes, purified according to the procedures of Marmur (1961) and Shields and Straus (1975), and "sheared" by sonication into fragments with an average length of ca. 500 nucleotides. Fragment size was determined by electrophoretic comparisons with DNA fragments of known size produced by the digestion of bacteriophage DNA with bacterial restriction endonucleases (Nathans and Smith 1975).

The single-stranded DNA fragments of the Red-eyed Vireo were allowed to reassociate to a C_ot of 1000 at 50°C in 0.48 M sodium phosphate buffer. (C_ot = the concentration of DNA in moles/liter × the duration of incubation in seconds [Kohne 1970:334].) This period of reassociation permitted most of the rapidly reassociating repeated sequences to form double-stranded molecules while the slowly reassociating single-copy sequences remained

single stranded. The latter were recovered by chromatography on a hydroxyapatite column. This process produced a single-copy DNA preparation consisting of one copy per genome of each original single-copy sequence and at least one copy per genome of each different repeated sequence. Such a single-copy preparation contains at least 98%, and probably 100%, of the "sequence complexity" of the genome, i.e., the total length of different DNA sequences (Britten 1971; R. J. Britten, pers. comm.). Kohne (1970:334–347) has discussed the reasons for using only single-copy DNA in studies designed to determine "the extent of nucleotide change since the divergence of two species."

The single-copy DNA sequences of the Red-eyed Vireo were labelled with radioactive iodine (^{125}I) according to the procedures of Commorford (1971) and Prensky (1976). DNA-DNA hybrids were formed from a mixture composed of one part (=250 ng) radioiodine-labelled single-copy DNA and 1000 parts (=250 μg) sheared, whole DNA. The hybrid combinations were heated to 100°C for 10 min to dissociate the double-stranded molecules into single strands, then incubated for 120 h (=C_0t 16,000) at 60°C to permit the single strands to form double-stranded hybrid molecules.

The DNA-DNA hybrids were bound to hydroxyapatite columns immersed in a temperature-controlled water bath at 55°C and the temperature was then raised in 2.5°C increments from 55°–95°C. At each of the 17 temperatures the single-stranded DNA produced by the melting of double-stranded hybrids was eluted in 20 ml of 0.12 M sodium phosphate buffer.

The radioactivity in each eluted sample was counted in a Packard Model 5220 Auto-Gamma Scintillation Spectrometer, optimized for ^{125}I. A teletype unit connected to the gamma counter printed out the data and punched a paper tape which is the entry to the computer program.

The computer program uses a non-linear regression least squares procedure to determine the best fit of the experimental data to one of four functions: (1) the Normal, (2) the dual-Normal, (3) the "skewed" Normal, or (4) a modified Fermi-Dirac. The $T_{50}H$ is the temperature above which less than 50% of the sequences will be hybridized, and below which more than 50% will be hybridized. This is, approximately, the median divergence point. The $T_{50}H$ is also the mode of a homologous hybrid and is equal to the mode of any hybrid if all single-copy sequences in the two species could form stable duplexes under the incubation conditions.

In each experimental set the labelled taxon is hybridized with itself (=homologous hybrid) and the differences in degrees Celsius between its $T_{50}H$ value and those of the heterologous hybrids are the delta $T_{50}H$ values. The $T_{50}H$ of Bonner et al. (1981) is the same as the $T_{50}R$ of Kohne (1970).

RESULTS AND DISCUSSION

Table 1 contains the distance values (delta $T_{50}H$) for DNA-DNA hybrids between the Red-eyed Vireo and 35 other species of passerine birds. The delta $T_{50}H$ values are measurements between the Red-eyed Vireo and the other taxa, but not among the other taxa, because only the DNA of the Red-eyed Vireo was labelled with radioiodine. Two taxa that have the same delta $T_{50}H$ values are equidistant from the labelled taxon but they can be any distance from one another which is equal to, or less than, their common distance from the labelled species. Only a complete matrix of DNA distance values provides the basis for the reconstruction of a phylogeny but a one-dimensional data set, as in Table 1, can reveal the degrees of relationship between the labelled species and other taxa.

Table 1

DNA-DNA Hybridization Values (delta $T_{50}H$) for Comparisons Between the Red-eyed Vireo and Other Species of Passerine Birds

Species	Delta $T_{50}H$	Group index[a]
Subfamily Vireoninae		
1. *Vireo olivaceus* (Red-eyed Vireo)	0.0	CV
2. *V. altiloquus* (Black-whiskered Vireo)	0.7	CV
3. *V. solitarius* (Solitary Vireo)	2.5	CV
4. *V. solitarius* (Solitary Vireo)	2.7	CV
5. *V. griseus* (White-eyed Vireo)	2.9	CV
6. *Hylophilus ochraceiceps* (Tawny-crowned Greenlet)	3.2	CV
7. *H. flavipes* (Scrub Greenlet)	3.5	CV
8. *Cyclarhis gujanensis* (Rufous-browed Peppershrike)	4.1	CV
9. *C. gujanensis* (Rufous-browed Peppershrike)	4.2	CV
Other members of the "corvine assemblage"		
10. *Coracina novaehollandiae* (Large Cuckoo-shrike)	7.5	CC
*11. *Grallina cyanoleuca* (Australian Magpie-lark)	7.5	CM
12. *Dicrurus paradiseus* (Paradise Drongo)	7.8	CM
*13. *Monarcha guttula* (Spot-winged Monarch)	7.8	CM
14. *Pica pica* (Black-billed Magpie)	8.2	CC
*15. *Corvus brachyrhynchos* (Common Crow)	8.9	CC
16. *Aegithina tiphia* (Common Iora)	9.2	C?
*17. *Corvus brachyrhynchos* (Common Crow)	9.4	CC
*18. *Lanius collurio* (Red-backed Shrike)	9.4	CC
Members of other oscine families		
19. *Zonotrichia albicollis* (White-throated Sparrow)	10.7	FP
20. *Geothlypis trichas* (Common Yellowthroat)	10.8	FP
*21. *Ploceus capensis* (Cape Weaver)	11.0	FP
*22. *Nectarinia jugularis* (Olive-backed Sunbird)	11.1	FP
*23. *Motacilla alba* (White Wagtail)	11.2	FP
24. *Irena puella* (Fairy Bluebird)	11.4	?
25. *Lonchura bicolor* (Bronze Mannikin)	11.4	FP
*26. *Polioptila melanura* (Black-tailed Gnatcatcher)	11.4	ST
*27. *Passer domesticus* (House Sparrow)	11.5	FP
*28. *Trichastoma bicolor* (Ferruginous Jungle-Babbler)	11.7	ST
*29. *Sturnus vulgaris* (Common Starling)	12.2	MT
30. *Meliphaga flaviventer* (Buff-breasted Honeyeater)	12.4	AWH
*31. *Mimus polyglottos* (Northern Mockingbird)	12.5	MT
*32. *Zosterops pallida* (Pale White-eye)	12.8	ST
*33. *Parus major* (Great Tit)	13.2	ST
*34. *Troglodytes aedon* (House Wren)	13.2	ST
*35. *Turdus migratorius* (American Robin)	13.3	MT
36. *Ficedula dumetoria* (Orange-breasted Flycatcher)	13.3	MT
*37. *Sylvia atricapilla* (Blackcap)	13.5	ST
Suborder Tyranni		
*38. *Elaenia flavogaster* (Yellow-bellied Elaenia)	16.1	SO

[a] Group index abbreviations are: CV = Corvine-Vireonine; CC = Corvine-Corvine; CM = Corvine-Monarchine; FP = Fringillid-Ploceid; ST = Sylviine-Timaliine; MT = Muscicapine-Turdine; AWH = Australian Warbler-Honeyeater; SO = Suboscine; ? = uncertain.

* Indicates that the taxon has been used as the "labelled" species in another study.

From other studies (Sibley and Ahlquist 1980, 1981a–c, 1982b, c, in press a–c) we have found that (1) congeneric species commonly have delta $T_{50}H$ values up to ca. 3.0, (2) members of the same subfamily may differ by delta $T_{50}H$ values up to ca. 6.0, (3) members of the same family may differ by delta values up to ca. 9, and (4) species in different families of the same superfamily differ by delta $T_{50}H$ values between ca. 10 and 14. These estimates may vary by ±1.0 and delta $T_{50}H$ values have an average experimental error of ±0.5.

The delta $T_{50}H$ values in Table 1 indicate that *Vireo*, *Hylophilus* and *Cyclarhis* are closely related and may be included in the same subfamily. The delta $T_{50}H$ value for the Red-eyed Vireo × Black-whiskered Vireo hybrid (0.7) reflects the close relationship between these species. Mayr and Short (1970:72) include them in the same superspecies and note that *V. altiloquus* is "essentially the West Indian representative of *olivaceus* . . . ."

The taxa in Table 1 with delta $T_{50}H$ values from 7.5 (*Coracina*) to 9.4 (*Lanius*) are members of a large "corvine assemblage," the boundaries of which are not yet completely delineated. The group seems primarily to be Australasian and, in addition to the taxa represented in Table 1, it includes the Old World orioles (Oriolidae), the birds of paradise (Paradisaeidae), the Australo-Papuan bell-magpies and butcherbirds (Cracticidae) and the woodswallows (*Artamus*).

The taxa in Table 1 with delta $T_{50}H$ values from 10.7 (*Zonotrichia*) to 13.5 (*Sylvia*) are members of other families of the suborder Passeres. *Zonotrichia* and *Geothlypis* are representatives of the subfamily Emberizinae, family Fringillidae (Sibley 1970, Sibley and Ahlquist 1982b) and *Ploceus*, *Nectarinia*, *Motacilla*, *Lonchura*, and *Passer* are also members of the fringillid-ploceid assemblage (Sibley and Ahlquist 1980, 1981b, c). *Trichastoma* and *Sylvia* are members of the Sylviidae and *Parus* is related to them (Sibley and Ahlquist 1980, 1982c). *Sturnus*, *Mimus*, *Turdus* and *Ficedula* are members of a muscicapoid assemblage which includes the muscicapine flycatchers, erithacine thrushes, dippers (*Cinclus*), starlings, mockingbirds (*Mimus*) and thrashers (*Toxostoma*) and the turdine thrushes (Sibley and Ahlquist 1980, 1982c). The honeyeaters (e.g., *Meliphaga*) are members of an Australasian group that includes the acanthizine warblers (*Acanthiza*, etc.) and the fairy-wrens (*Malurus*, etc.) (Sibley and Ahlquist, in press b, c). The suboscine flycatcher, *Elaenia*, is a member of the family Tyrannidae.

The DNA hybridization data in the papers cited above provide a more extensive matrix of DNA distance values and have made it possible for us to define the principal clusters and the branching pattern of the taxa in Table 1. The results are diagrammed in Fig. 1.

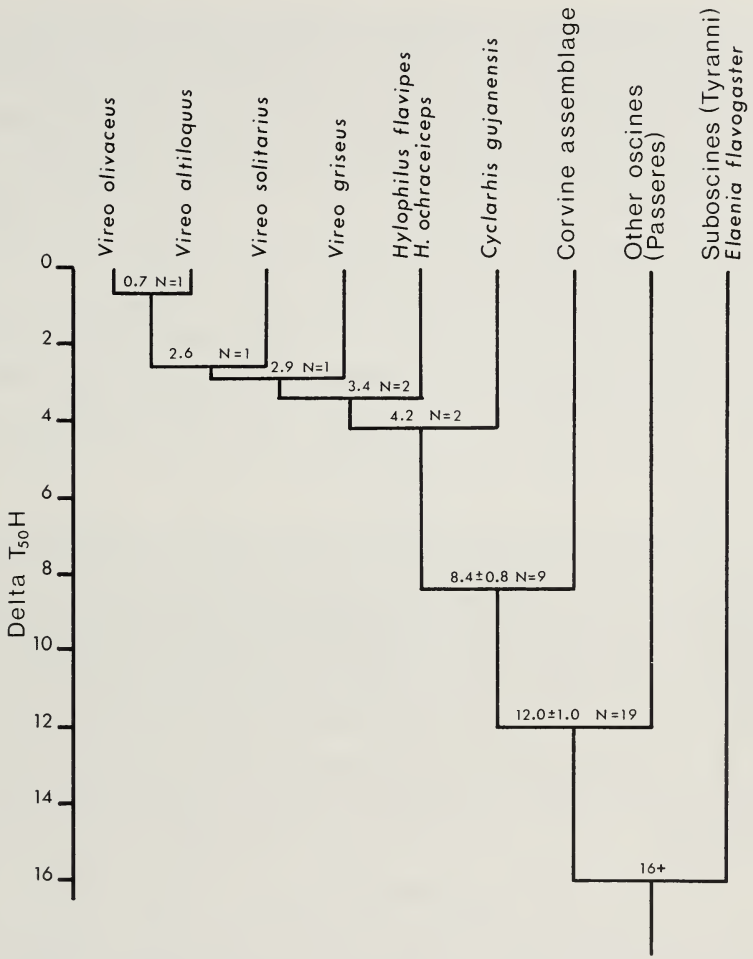


FIG. 1. Diagram based on the $T_{50}H$ values in Table 1. See text for explanation.

Each of the members of the vireonine cluster in Fig. 1 diverged from the lineage leading to *V. olivaceus* via different branch nodes; hence they form a nesting series of sister groups from *V. altiloquus* at delta $T_{50}H$ 0.7 to *Cylarhis* at 4.2. From the other studies cited above we know that the "corvine assemblage" includes the taxa in Table 1 with delta $T_{50}H$ values from 7.5–9.4. Since these are clustered within a range of 1.9 delta $T_{50}H$ units we may assume that this cluster is the sister group of the vireonines and we can therefore use the average delta $T_{50}H$ value (8.4 ± 0.8 SD) as the index to the divergence between these two clusters. Similarly, the

cluster of "other oscines" in Table 1 and Fig. 1 is the sister group of the combined vireonine and corvine clusters. The 19 genera in the cluster of "other oscines" represent 16 of Wetmore's (1960) families and have an average delta $T_{50}H$ of 12.0 ± 1.0 from *V. olivaceus*. Thus, although we may safely assume that these 16 families branched from one another over a span of at least several million years, they are all essentially the same delta $T_{50}H$ distance from the labelled species *V. olivaceus*. Furthermore, the corvine-vireonine lineage obviously branched from the "other oscines" lineage before these 16 families branched from one another.

We have found this same pattern of clustering and branching in all of our studies using DNA-DNA hybridization (cited above). This pattern indicates that all living taxa on one branch of a divergence node will be equidistant from all living taxa on the other branch of that node, i.e., all members of sister group A are equidistant from all members of sister group B, and vice versa. This is the "relative rate test" of Sarich and Wilson (1967).

We interpret this consistent pattern in the data as evidence that the average rate of DNA evolution (i.e., nucleotide substitution) is the same in all lineages of birds. This uniform average rate is apparently the statistical result of the large number of nucleotides in the avian haploid genome, viz., ca. 1.7×10^9. Each sequence evolves at its own rate and different sequences evolve at different rates at different times and in different species, but when averaged over the genome, and over time, the uniform average rate is the inevitable result because there are upper and lower bounds to the rates and their frequency distribution is narrow relative to the number of nucleotides.

The uniform average rate means that the DNA-DNA hybridization values are directly proportional to relative time and, therefore, may be used to reconstruct phylogenies. If they can be calibrated against geological or fossil dates, the DNA values can be correlated with absolute time. We have made some preliminary correlations (Sibley and Ahlquist 1981a), but the available datings are of uncertain accuracy and, so far, add little to the interpretation of the data. We urgently need accurate datings of the divergences between living lineages of birds.

We conclude that the typical vireos (*Vireo*), greenlets (*Hylophilus*), peppershrikes (*Cyclarhis*) and, presumably, shrike-vireos (*Vireolanius*) are members of the same subfamily, Vireoninae. It is not yet clear to which family the Vireoninae should be assigned but they are part of the corvine assemblage and are not closely related to the New World nine-primaried oscines. Additional support for this conclusion was obtained during a DNA-DNA hybridization study of the Hawaiian honeycreepers (Fringilli-

dae: Carduelinae: Drepanidini) in which a DNA-DNA hybrid between the radioiodine-labelled single-copy DNA of the Apapane (*Himatione sanguinea*) and the DNA of *V. olivaceus* had a delta $T_{50}H$ of 11.3 (Sibley and Ahlquist 1982a). Similarly, a DNA hybrid between the labelled DNA of the Yellow-breasted Chat (*Icteria virens:* Fringillidae: Emberizinae: Parulini) and the DNA of *V. olivaceus* had a delta mode of 10.4 (Sibley and Ahlquist 1982b).

Avise et al. (1980) also demonstrated the large genetic gap between the vireos and the wood warblers by their electrophoretic comparisons of 16 proteins among 12 genera of paruline warblers, a turdine thrush (*Catharus*) and the Red-eyed Vireo. They found that the thrush, although itself quite distant from the wood warblers, was closer to them than was the vireo. We have discussed this study in more detail elsewhere (Sibley and Ahlquist 1982b).

SUMMARY

The relationships of the vireos (Vireoninae) have been debated for more than a century. The shrikes (Laniidae) and the New World nine-primaried oscines have been most frequently proposed as their closest relatives. Comparisons were made between the single-copy DNA sequences of the Red-eyed Vireo (*Vireo olivaceus*) and those of 34 other species representing other vireonines and the major taxa of passerine birds. *Vireo*, *Hylophilus* and *Cyclarhis* were found to be closely enough related to one another to be placed in the same subfamily. Their next nearest relatives are the members of the large and varied "corvine assemblage" which includes the cuckoo-shrikes, drongos, monarch flycatchers, crows, shrikes and several other taxa.

The vireos are not closely related to the New World nine-primaried oscines. The belief in this alliance, which has been accepted for the past 50 years, was based upon the incorrect interpretation of the reduction of the outer (10th) primary and other morphological characters.

ACKNOWLEDGMENTS

For assistance in the laboratory we thank C. Barkan, M. Pitcher, N. Snow, L. Feret, L. Merritt and F. C. Sibley. The computer program was written by T. F. Smith. For advice we are indebted to R. J. Britten, T. I. Bonner, D. E. Kohne, R. Holmquist, G. F. Shields, H. E. Burr, W. M. Fitch and W. F. Thompson. For assistance in the field we appreciate the help of H. L. Achilles, M. Bull, J. duPont, J. R. Ford, P. Garayalde, R. Liversidge, J. P. O'Neill, T. Osborne, S. Parker, W. S. Peckover, G. B. Ragless, R. Schodde, R. Semba, F. Sheldon, F. C. Sibley, J. Spendelow, N. and E. Wheelwright, and D. Wysham.

The laboratory work was supported by Yale University and the National Science Foundation (DEB–77–02594 and DEB–79–26746).

LITERATURE CITED

Averill, C. K. 1925. The outer primary in relation to migration in the ten-primaried oscines. Auk 42:353–358.

Avise, J. C., J. C. Patton and C. F. Aquadro. 1980. Evolutionary genetics of birds.

Comparative molecular evolution in New World warblers and rodents. J. Heredity 71:303–310.

Baird, S. F. 1858. U.S. Pacific railroad surveys. Vol. 9, Pt. 2, Birds. Washington, D.C.

———. 1864. Review of American birds, Pt. 1. Smithson. Misc. Coll. 181.

Barlow, J. C. and R. D. James. 1975. Aspects of the biology of the Chestnut-sided Shrike-Vireo. Wilson Bull. 87:320–334.

Beecher, W. J. 1953. A phylogeny of the oscines. Auk 70:270–333.

Blake, E. R. 1968. Vireonidae. Pp. 103–138 *in* Peters check-list of birds of the world, Vol. 14 (R. A. Paynter, Jr., ed.). Mus. Comp. Zool., Cambridge, Massachusetts.

Bock, W. J. 1960. The palatine process of the premaxilla in the Passeres. Bull. Mus. Comp. Zool. 122:361–488.

———. 1962. The pneumatic fossa of the humerus in the Passeres. Auk 79:425–443.

Bonner, T. I., R. Heinemann and G. J. Todaro. 1981. A geographic factor involved in the evolution of the single copy DNA sequences of primates. Pp. 293–300 *in* Evolution today, Proc. II Int. Congr. Syst. Evol. Biol. (G. G. E. Scudder and J. L. Reveal, eds.). Hunt Inst. Botan. Document., Carnegie-Mellon Univ., Pittsburgh, Pennsylvania.

Britten, R. J. 1971. Sequence complexity, kinetic complexity, and genetic complexity. Carnegie Instit. Washington Yearbook 69:503–506.

——— and D. E. Kohne. 1968. Repeated sequences in DNA. Science 161:529–540.

———, D. E. Graham and R. B. Neufeld. 1974. Analysis of repeating DNA sequences by reassociation. Pp. 363–418 *in* Methods in enzymology, Vol. 29 (L. Grossman and K. Moldave, eds.). Academic Press, New York, New York.

Commorford, S. L. 1971. Iodination of nucleic acids *in vitro*. Biochem. 10:1993–2000.

Coues, E. 1892. Key to North American birds. 4th ed. Estes and Lauriat, Boston, Massachusetts.

Deignan, H. G. 1964. Subfamily Panurinae. Pp. 430–442 *in* Peters check-list of birds of the world, Vol. 10 (E. Mayr and R. A. Paynter, Jr., eds.). Mus. Comp. Zool., Cambridge, Massachusetts.

Gadow, H. 1883. Catalogue of the birds in the British Museum, Vol. 8. Trustees, British Museum, London, England.

Hamilton, T. H. 1958. Adaptive variation in the genus *Vireo*. Wilson Bull. 70:307–346.

———. 1962. Species relationships and adaptations for sympatry in the avian genus *Vireo*. Condor 64:40–68.

Hellmayr, C. E. 1935. Catalogue of birds of the Americas and the adjacent islands, Vol. 13, Pt. 8. Field Mus. Nat. Hist. Publ. 347, Zool. Ser.

Kohne, D. E. 1970. Evolution of higher-organism DNA. Quart. Rev. Biophysics 33:327–375.

Marmur, J. 1961. A procedure for the isolation of deoxyribonucleic acid from micro-organisms. J. Mol. Biol. 3:208–218.

Mayr, E. and D. Amadon. 1951. A classification of recent birds. Am. Mus. Novit. 1496: 1–32.

——— and L. L. Short, Jr. 1970. Species taxa of North American birds. Publ. Nutt. Ornithol. Club. No. 9. Cambridge, Massachusetts.

Nathans, D. and H. O. Smith. 1975. Restriction endonucleases in the analysis and restructuring of DNA molecules. Ann. Rev. Biochem. 44:273–293.

Naumburg, E. M. B. 1925. A few remarks about *Cyclarhis gujanensis cearensis*. Auk 42:341–349.

Orenstein, R. I. and J. C. Barlow. 1981. Variation in the jaw musculature of the avian family Vireonidae. Life Sci. Contrib. Roy. Ont. Mus. 128.

Parker, W. K. 1878. On the skull of the aegithognathous birds, Pt. 2. Trans. Zool. Soc. London 10(6):251–314.

PRENSKY, W. 1976. The radioiodination of RNA and DNA to high specific activities. Pp. 121–152 *in* Methods in cell biology, Vol. 13 (D. M. Prescott, ed.). Academic Press, New York, New York.

PYCRAFT, W. P. 1907. Contributions to the osteology of birds, Pt. 9, Tyranni; Hirundines; Muscicapae; Lanii, and Gymnorhines. Proc. Zool. Soc. London 1907:352–379.

RAIKOW, R. J. 1978. Appendicular myology and relationships of the New World nine-primaried oscines (Aves: Passeriformes). Bull. Carnegie Mus. Nat. Hist. 7:1–43.

RIDGWAY, R. 1904. The birds of North and Middle America, Pt. 3. Bull. U.S. Natl. Mus. 50.

SARICH, V. M. AND A. C. WILSON. 1967. Immunological time scale for hominoid evolution. Science 158:1200–1203.

SCLATER, P. L. AND O. SALVIN. 1873. Nomenclator avium neotropicalium. London, England.

SHIELDS, G. F. AND N. A. STRAUS. 1975. DNA-DNA hybridization studies of birds. Evolution 29:159–166.

SIBLEY, C. G. 1970. A comparative study of the egg-white proteins of passerine birds. Bull. Peabody Mus. Nat. Hist. 32.

——— AND J. E. AHLQUIST. 1980. The relationships of the "primitive insect eaters" (Aves: Passeriformes) as indicated by DNA-DNA hybridization. Pp. 1215–1220 *in* Proc. XVII Int. Ornithol. Congr.

——— AND ———. 1981a. The phylogeny and relationships of the ratite birds as indicated by DNA-DNA hybridization. Pp. 301–335 *in* Evolution today, Proc. II Int. Congr. Syst. Evol. Biol. (G. G. E. Scudder and J. L. Reveal, eds.). Hunt Inst. Botanic. Document., Carnegie-Mellon Univ., Pittsburgh, Pennsylvania.

——— AND ———. 1981b. The relationships of the wagtails and pipits (Motacillidae) as indicated by DNA-DNA hybridization. L'Oiseau et R.F.O.

——— AND ———. 1981c. The relationships of the Accentors (*Prunella*) as indicated by DNA-DNA hybridization. J. Orn. 122:369–378.

——— AND ———. 1982a. The relationships of the Hawaiian honeycreepers (Drepaninini) as indicated by DNA-DNA hybridization. Auk 99:130–140.

——— AND ———. 1982b. The relationships of the Yellow-breasted Chat (*Icteria virens*), and the alleged "slow-down" in the rate of macromolecular evolution in birds. Postilla 187:1–19.

——— AND ———. 1982c. The relationships of the Wrentit (*Chamaea fasciata*) as indicated by DNA-DNA hybridization. Condor 84:40–44.

——— AND ———. In press a. The relationships of the Australo-Papuan scrub-robins *Drymodes* as indicated by DNA-DNA hybridization. Emu.

——— AND ———. In press b. The relationships of the Australo-Papuan fairy-wrens as indicated by DNA-DNA hybridization. Emu.

——— AND ———. In press c. The relationships of the Australasian whistlers *Pachycephala* as indicated by DNA-DNA hybridization. Emu.

STALLCUP, W. B. 1954. Myology and serology of the avian family Fringillidae. Publ. Mus. Nat. Hist. Univ. Kansas 8(2):157–211.

———. 1961. Relationships of some families of the suborder Passeres (songbirds) as indicated by comparisons of tissue proteins. J. Grad. Res. Center, Southern Methodist Univ. 29:43–65.

STEGMANN, B. 1962. Die verkummerte distale Handschwinge des Vogelflügels. J. Orn. 103:50–85.

SUNDEVALL, C. J. 1872. Methodi naturalis avium disponendarum tentamen. Samson and Wallin, Stockholm, Sweden. Eng. transl., F. Nicholson, 1889. R. H. Porter, London, England.

THOMSON, A. L., (ED.). 1964. A new dictionary of birds. Thomas Nelson and Sons, London, England.

TORDOFF, H. B. 1954a. A systematic study of the avian family Fringillidae based on the structure of the skull. Misc. Publ. Mus. Zool. Univ. Mich. No. 81.

———. 1954b. Relationships in the New World nine-primaried oscines. Auk 71:273–284.

WETMORE, A. 1930. A systematic classification for the birds of the world. Proc. U.S. Natl. Mus. 76(24):1–8.

———. 1951. A revised classification for the birds of the world. Smithson. Misc. Coll. 117(4):1–22.

———. 1960. A classification for the birds of the world. Smithson. Misc. Coll. 139(11):1–37.

ZIMMER, J. T. 1942. Studies of Peruvian birds. No. XLI. The genera *Hylophilus*, *Smaragdolanius*, and *Cyclarhis*. Am. Mus. Novit. 1160:1–16.

PEABODY MUSEUM OF NATURAL HISTORY AND DEPT. BIOLOGY, YALE UNIV., NEW HAVEN, CONNECTICUT 06511. ACCEPTED 7 OCT. 1981.

Wilson Bull., 94(2), 1982, pp. 129–138

VEGETATION RELATIONSHIPS AND FOOD OF SAGE SPARROWS WINTERING IN HONEY MESQUITE HABITAT

Julie K. Meents, Bertin W. Anderson and Robert D. Ohmart

The breeding habitat and behavior of Sage Sparrows (*Amphispiza belli*) have been documented by a number of investigators (Linsdale 1938, Miller 1968, Feist 1972, Rotenberry and Wiens 1978, Rich 1980). Although the breeding season is important to birds, conditions on wintering grounds may have a primary role in regulating populations of migratory species such as the Sage Sparrow (Fretwell 1972). Previously published information concerning wintering Sage Sparrows consists of general comments on distribution, habitat and food (Goss 1881, van Rossem 1911, Miller 1968).

Sage Sparrows usually arrive in the lower Colorado River valley during September and remain until February or early March. The species occurs in most riparian habitats, but the greatest number of sparrows is consistently found in vegetation dominated by honey mesquite (*Prosopis glandulosa*). Within honey mesquite habitat, Sage Sparrows tend to concentrate in certain areas.

Our primary purpose in this study was to identify aspects of riparian vegetation that consistently attracted Sage Sparrows. We did this by examining annual and seasonal variation in distribution of the Sage Sparrow population in the lower Colorado River valley. We also examined food use to determine if there were associations between Sage Sparrows and specific types of resources.

We found that presence of inkweed (*Suaeda torreyana*) characterized areas where the number of Sage Sparrows was greater than the average for all areas. To test the relationship of Sage Sparrows and inkweed, we planted three sites with different densities of inkweed and other shrubs. Evidence from these sites supports the conclusion that inkweed is actively selected by wintering Sage Sparrows.

METHODS

As part of a project evaluating wildlife use of riparian habitats, we established 72 transects (800 or 1600 m long) in representative riparian vegetation along the lower Colorado River from the Mexican border north to Davis Dam, on the Nevada-Arizona border. The transects covered the ranges of vegetation composition and vertical configuration present in the area. Each transect was placed in a relatively homogeneous stand of vegetation. General habitat types were identified by the dominant tree or shrub (if there were no trees) present in the stand. These habitats included screwbean mesquite (*Prosopis pubescens*), cottonwood (*Populus fremontii*)-willow (*Salix gooddingii*), salt cedar (*Tamarix chinensis*), honey mesquite,

arrowweed (*Tessaria sericea*) and salt cedar-honey mesquite. Twenty of the transects were in honey mesquite vegetation in a 6000-ha area between Parker and Ehrenberg, Yuma Co., Arizona. All transects were censused two or three times per month using a modification of the Emlen (1971) variable distance method. Sage Sparrow data were collected between September and February each year from 1975–1980. Computer simulation has indicated that 6–9 censuses are necessary to obtain accurate population estimates (Engel-Wilson et al. 1981), so we considered "seasonal" data when making calculations such as distributional diversity and correlations of bird densities with vegetation variables. The fall season included September through November; winter included December through February. Seasonal densities of Sage Sparrows are the average of all censuses in each period.

Sage Sparrow distributional diversity among the 20 honey mesquite transects was calculated using $H = -\Sigma\, p_i \log_{10} p_i$, where p_i is the proportion of the total number of Sage Sparrows occurring on each transect (densities standardized to 40 ha). The extent to which the sparrows were equally abundant on all transects (evenness) equalled the proportion of maximum possible H ($H/\log_{10} N$, where N = total number of transects). Significance of differences in H was tested following Zar's (1974) method for diversity indices.

All trees and shrubs within 15 m of both sides of each transect were counted; densities were extrapolated to number per ha. Foliage indices, including foliage density (DEN), patchiness (PI) and foliage height diversity (FHD) were derived from measurements obtained with the board technique (MacArthur and MacArthur 1961). Our patchiness index represents the variance (S^2) associated with foliage density in 150-m units along each side of a transect. Further details of vegetation measurement techniques are available in Anderson et al. (1977, 1978). Initial vegetation measurements made in the summer of 1975 were used to characterize the vegetation available to Sage Sparrows in the falls and winters of 1975–76 and 1976–77. Measurements were repeated in summer 1977 and 1979; these values were used in examining Sage Sparrow habitat relationships in the subsequent falls and winters. We felt that it was valid to use vegetation measurements taken in one year to characterize the transects for several subsequent years because there was little change in most vegetation measurements between years. For example, not a single measurement taken in 1979 differed significantly from those for 1977. Measurements made on green foliage in summer reflect the density of nondeciduous foliage and/or leaf-bearing twigs in winter (Anderson and Ohmart, unpubl.). Vegetation variables considered in analyses included density of honey mesquite trees, densities of *Atriplex* spp. and inkweed shrubs, foliage DEN 0–0.6 m, total foliage DEN, PI 1.5–3.0 m, total PI and FHD. We chose these variables because they were not highly intercorrelated and described features of the vegetation that varied between transects.

A 2-tailed *t*-test tested differences in mean vegetation measurements between transects where Sage Sparrows occurred in below- and above-average numbers. Stepwise multiple regressions examined specific Sage Sparrow vegetation relationships. Data were transformed using square roots or $\log_{10}(N + 1)$ (Sokal and Rohlf 1969). Standardized vegetation variables were raised to the second, third and fourth powers in order to discern certain nonlinear functions that may be more appropriate for describing ecological relationships than simple linear functions (Green 1979; Meents et al., unpubl.). Regressions were terminated when additional significant variables accounted for <5% of the variance.

An index to relative insect biomass was obtained by weighing insects captured in a 4000-sweep sample on a transect in each habitat. The same transect was sampled in each habitat type each month in 1976 and 1977.

Three sites in the riparian floodplain of the lower Colorado River were manipulated to test the effect of changing the amount and structure of vegetation. None of these sites was used by Sage Sparrows prior to manipulation. Two areas (20 and 30 ha) were originally sandy dredge spoil that supported little vegetation. A third site (20 ha), originally covered by salt

Table 1
Average Characteristics of Sage Sparrow Populations and Distribution on Honey Mesquite Transects

	1975–76		1976–77		1977–78		1978–79		1979–80	
	FA[a]	WI[b]	FA	WI	FA	WI	FA	WI	FA	WI
$\bar{x}$ density	2.7	5.3	4.3	6.5	5.5	7.0	8.2	7.9	16.5	12.6
SE	±0.9	±3.5	±1.9	±3.9	±1.8	±2.9	±2.7	±3.8	±4.3	±2.8
Evenness	0.67	0.28	0.58	0.43	0.76	0.66	0.73	0.59	0.82	0.85
H	2.01	0.85	1.74	1.28	2.26	1.98	2.17	1.77	2.44	2.52
H change[c]	$P < 0.001$		$P < 0.01$		$P < 0.05$		$P < 0.001$		NS	

[a] FA = fall.
[b] WI = winter.
[c] Significance of difference in H between seasons (Zar 1974).

cedar, was cleared. All three areas were revegetated with native trees and shrubs, including cottonwood, willow, honey mesquite, palo verde (*Cercidium floridum*), wolfberry (*Lycium pallidum*), quail bush (*Atriplex lentiformis*) and inkweed (Anderson et al. 1978). Site I had no inkweed, site II had a small amount of inkweed and site III had a high density of inkweed. All areas were censused during fall 1980 and winter 1980–81.

RESULTS

Birds.—The average annual density of Sage Sparrows in honey mesquite habitat showed a gradual increase over the 5 years of study (Table 1). Mean densities increased from 2.7 birds/40 ha in fall 1975 to 16.5 birds/40 ha in fall 1979. A less dramatic increase occurred from winter 1975–76 (5.3 birds/40 ha) to winter 1979–80 (12.6 birds/40 ha).

Densities of Sage Sparrows in all other riparian habitats were very low between fall 1975 and winter 1978–79 (all habitats were not censused in 1979–80). Average densities for the 4 years were 0.28 (SE = ± 0.18) birds/40 ha in fall and 0.06 (SE = ± 0.03) birds/40 ha in winter. Because of these low densities only honey mesquite habitat was considered in further analyses.

Some transects regularly supported higher densities of Sage Sparrows. Five transects had above-average Sage Sparrow numbers in at least 2 years in fall; three of these were above average in all 5 years. In winter, four transects had above-average densities in at least 2 years; two of these were preferred in all 5 years. Two transects were above average in both seasons during all the years sampled.

Both distributional diversity and evenness of Sage Sparrows were reduced from fall to winter of each year, except in 1979–80 when differences between seasons were not significant (Table 1). This indicated that the

sparrow population became concentrated in a few areas as winter progressed.

In 1979–80, when distributional diversity and evenness were greatest, sparrow numbers were higher than in any previous year (Table 1). Densities in this year were above average on a number of transects where only below-average densities had occurred previously. This was especially apparent during winter. However, transects that had been consistently favored in previous years continued to support high densities of Sage Sparrows.

Vegetation.—The only statistically significant difference in vegetation between transects with above- and below-average densities of Sage Sparrows was in the number of inkweed shrubs (fall $P < 0.001$, winter $P < 0.01$). Inkweed in the lower Colorado River valley occurs primarily in patches within areas dominated by honey mesquite. Sage Sparrows also tended ($0.1 > P > 0.05$) to be absent from transects with high densities of honey mesquite trees and *Atriplex* spp. shrubs.

Seasonal vegetation relationships were examined with stepwise multiple regressions of Sage Sparrow numbers against all vegetation variables. Overall, relationships with the vegetation accounted for an average of 68% of the variation in Sage Sparrow densities (Table 2). Inkweed density was the first variable selected in 9 of 10 cases. Inkweed density alone accounted for an average of 50% of the variance and always showed a positive relationship with Sage Sparrow densities. The relationship was linear in only one case. Half of the times when inkweed was included as a significant step the square of inkweed density was chosen. When graphed, this produced a U-shaped curve, indicating that Sage Sparrows occurred on some transects that had no inkweed and were present in relatively low numbers on some transects that had intermediate densities of inkweed. The cube of inkweed density was included in three cases. This indicates a near-linear relationship between inkweed and Sage Sparrow densities, but some transects that had inkweed had a rather low number of Sage Sparrows.

The second variable chosen in the stepwise regression procedure was different between seasons (Table 2). Densities of honey mesquite and *Atriplex* spp. shrubs showed negative relationships; foliage patchiness and density measures had positive relationships with sparrow densities.

The reduction of sparrow distributional diversity between fall and winter was not paralleled by any consistent change in association with vegetation. Inkweed was the most important habitat component in both seasons.

Sage Sparrow densities varied among the three revegetated sites (Table 3). The areas that had little or no inkweed supported similarly low sparrow densities in both seasons ($\bar{x}$ = 2.8 birds/40 ha). The area with a relatively

Table 2

Summary of Stepwise Multiple Regressions Between Sage Sparrow Densities and Honey Mesquite Vegetation Variables

Year/season	Vegetation variables[a] Step to enter 1	2	3	4	Total R^2
1975–76					
Fall	inkweed[2]	-mesquite[4]	FHD[3]	DEN 0–0.6[4]	
	0.34	0.07	0.16	0.05	0.62
Winter	inkweed[3]	PI sum[4]			
	0.67	0.05	—	—	0.72
1976–77					
Fall	inkweed	-*Atriplex*[4]			
	0.72	0.10	—	—	0.82
Winter	inkweed[4]	-*Atriplex*			
	0.66	0.09	—	—	0.75
1977–78					
Fall	inkweed[3]	PI sum[4]			
	0.40	0.10	—	—	0.50
Winter	inkweed[2]	PI 1.5–3[4]			
	0.62	0.06	—	—	0.68
1978–79					
Fall	inkweed[2]	-mesquite	-mesquite[4]		
	0.41	0.23	0.10	—	0.74
Winter	inkweed[2]				
	0.73	—	—	—	0.73
1979–80					
Fall	-mesquite	inkweed[2]	DEN 0–0.6		
	0.35	0.19	0.06	—	0.60
Winter	inkweed[3]	-DEN sum	-DEN sum[4]	PI 1.5–3[4]	
	0.21	0.17	0.14	0.09	0.61
Mean R^2					0.68

[a] Numbers below variables are R^2 for the first step and R^2 change for subsequent steps.

high density of inkweed also had a high density of Sage Sparrows ($\bar{x}$ = 46.5 birds/40 ha).

Diet.—Insect biomass in riparian habitats of the lower Colorado River valley showed seasonal cycles of abundance (Fig. 1). Insect biomass declined throughout late summer, fall and winter; a similar pattern occurred in honey mesquite habitat.

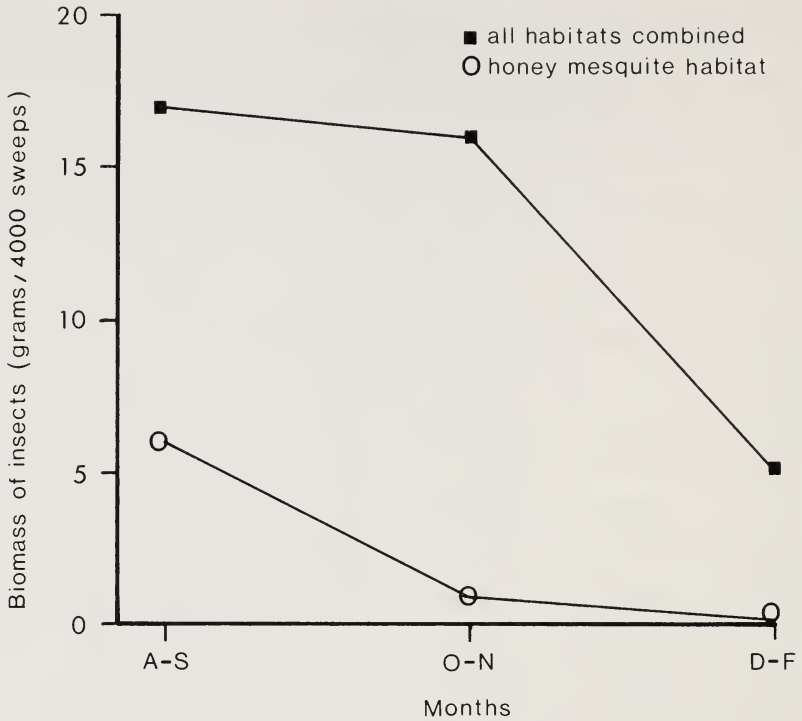


FIG. 1. Average insect biomass in riparian habitats of the lower Colorado River valley; A–S = August–September, O–N = October–November, D–F = December–February.

Analysis of gizzard and esophageal contents of Sage Sparrows collected in honey mesquite habitat also indicated seasonal changes (Table 4). In fall, animal material constituted an average of 44% of the volume of sparrow stomach contents; the remaining 56% was seed and plant material.

TABLE 3

DENSITIES OF *ATRIPLEX LENTIFORMIS*, INKWEED AND SAGE SPARROWS ON THREE MANIPULATED SITES

Site	Shrubs (no./ha)		Sage Sparrows (no./40 ha)	
	Atriplex	inkweed	fall 1980	winter 1980–81
I	7.6	0.0	3.5	2.7
II	40.0	0.8	2.0	3.0
III	134.0	23.9	30.5	62.0

TABLE 4
RESULTS OF STOMACH ANALYSES OF SAGE SPARROWS COLLECTED IN HONEY MESQUITE HABITAT

Season	N	Material	% occurrence[a]	% volume[a]
Fall	8	Coleoptera	28.4	17.7
		Hemiptera	7.8	9.1
		Homoptera	3.9	1.1
		Orthoptera	3.9	1.7
		Formicidae	14.3	6.4
		Unidentified insect	3.9	8.4
Subtotal			62.2	44.4
		Chenopodiaceae seed	7.8	5.2
		Unidentified seed	3.9	3.3
		Unidentified plant	26.0	47.2
Subtotal			37.8	55.7
Winter	12	Coleoptera	4.2	1.3
		Homoptera	2.1	0.8
		Lepidoptera	2.8	5.6
		Formicidae	7.7	2.5
		Unidentified insect	10.8	2.5
Subtotal			27.5	12.7
		Chenopodiaceae seed	3.8	0.5
		Unidentified seed	11.5	4.2
		Unidentified plant	55.0	81.3
Subtotal			70.0	86.0
		Feather	2.1	1.3

[a] Columns do not add to 100.0 because of rounding.

Stomach contents of Sage Sparrows collected in winter had only 13% animal material; the rest consisted mostly of plants and seeds.

DISCUSSION

The gradual increase in the Sage Sparrow population over the 5 years of study was part of a general trend observed for many avian species in the lower Colorado River valley (Anderson and Ohmart, unpubl.). This increase was apparently related to the series of relatively mild winters and favorable food resources that followed the particularly severe winter of 1974–75. The population increase could also have been due to increased breeding success or resource or climatic conditions in other parts of the Sage Sparrow range that resulted in more birds wintering in the lower Colorado River valley.

Sage Sparrows occurred in honey mesquite habitat more frequently than

in other riparian habitats. As has been shown, this relationship was incidental since Sage Sparrows were associated with inkweed, which in the lower Colorado River valley occurs mostly in honey mesquite habitat. Site III of our vegetation manipulation study had high densities of inkweed and Sage Sparrows, but essentially no honey mesquite because at the time of this study, newly planted trees were <1 m tall and contributed minimally to the vegetation.

The observed distribution restriction between fall and winter and the overall association with inkweed may be explained by at least two nonexclusive alternatives. Sage Sparrows are almost exclusively insectivorous on their sagebrush (*Artemisia* spp.) breeding ground (Wiens and Rotenberry 1979) and the wintering population in the lower Colorado River valley consumed proportionately fewer insects throughout fall and winter. These seasonal changes were probably related to reduced insect availability accompanying the onset of winter. Incidental behavioral observations showed birds frequently feeding near or under inkweed. The shift to vegetation and seeds as primary food sources when there was a restriction of Sage Sparrows to inkweed areas suggests that inkweed is an important food in winter. Weather was mild in the one winter (1979–80) when sparrows did not show distribution restriction from fall to winter. Mild winters in the lower Colorado River valley have higher insect populations than harsh winters (Anderson and Ohmart, unpubl.). Abundant food resources and moderate temperatures may have allowed Sage Sparrows to winter in previously unsuitable areas.

Fretwell (1972) suggested that migratory birds may benefit if they winter in habitats resembling their breeding grounds (or choose breeding habitat that is similar to winter habitat, if winter conditions limit population size). Winter experience in inkweed areas may enhance reproduction and/or survival of Sage Sparrows on their structurally similar sagebrush breeding grounds (or vice versa). However, Sage Sparrows were not found in significant numbers in other vegetation of physiognomy similar to sagebrush. In particular, sparrow densities on honey mesquite transects and manipulated sites did not show a positive relationship with *Atriplex* spp. shrubs, so general structural features alone are apparently not responsible for the distribution of Sage Sparrows in their winter habitat.

Although there was clearly an association between Sage Sparrows and inkweed, this relationship was not simple, as evidenced by the selection of nonlinear variables in the regressions. It is unlikely that sparrows respond to only one aspect of their habitat, and their association with inkweed is undoubtedly modified by other factors. Some transects with inkweed also had high densities of honey mesquite and *Atriplex* spp. shrubs; both of these are apparently avoided by Sage Sparrows. These transects

account for the lower than expected number of Sage Sparrows on some transects that had inkweed.

The appearance in 1979–80 of above-average numbers of Sage Sparrows on transects that did not have a significant amount of inkweed supports the model of habitat selection and distribution proposed by Fretwell and Lucas (1969). According to this model, at low total population size only the highest quality habitat is occupied. But, as density increases, the relative quality of the habitat decreases, until a point is reached at which another habitat type is of equal quality. During the first two winters of this study, when density of sparrows was low, above-average numbers of Sage Sparrows were limited to transects with inkweed. In the subsequent 2 years, densities increased and above-average numbers of sparrows were found on one transect not having inkweed in each winter. During the fifth year of the study, when sparrows were most abundant, above-average densities of Sage Sparrows occurred on four transects that did not have inkweed. Despite the fact that the total sparrow population increased by almost 60% between winter 1978–79 and winter 1979–80, the average density on transects with inkweed remained about the same. Thus, the "excess" birds in the population in 1979–80 were using portions of the habitat that had not been selected when the population was lower.

Whether habitat selection by wintering Sage Sparrows is based on food, vegetation structure or some other resource, it is apparent that the sparrows prefer vegetation with inkweed as a significant component. Presence of Sage Sparrows in areas lacking inkweed appears to be largely restricted to those times when food resource conditions are most favorable (fall and mild winters) or when sparrow numbers are high. Under the more physiologically demanding conditions of winter or generally harsh years, the wintering Sage Sparrow population of the lower Colorado River valley concentrates in areas with relatively high densities of inkweed.

SUMMARY

Overwintering Sage Sparrows (*Amphispiza belli*) were studied for 5 years (1975–1980) in honey mesquite-dominated vegetation of the lower Colorado River valley. Distributional diversity and evenness were reduced between fall and winter of each year. There was also a dietary shift from animal to plant material between seasons. Areas that consistently supported above-average populations had more inkweed shrubs. Results from three sites with controlled vegetation parameters suggest that Sage Sparrows actively select inkweed.

ACKNOWLEDGMENTS

We would like to thank Dr. J. Rice for advice on statistical analysis. A. K. Webb provided computer assistance and C. D. Zisner typed the manuscript. S. M. Cook and J. R. Durham made helpful editorial suggestions. We are grateful to the numerous field biologists who collected data for this study. The project was supported by Bureau of Reclamation Contract No. 7–07–30–V0009.

LITERATURE CITED

Anderson, B. W., R. W. Engel-Wilson, D. Wells and R. D. Ohmart. 1977. Ecological study of southwestern riparian habitats: techniques and data applicability. USDA For. Serv. Gen. Tech. Rept. RM–43:146–155.

———, R. D. Ohmart and J. Disano. 1978. Revegetating the riparian floodplain for wildlife. USDA For. Serv. Gen. Tech. Rept. WO–12:318–331.

Emlen, J. T. 1971. Population densities of birds derived from transect counts. Auk 88:323–342.

Engel-Wilson, R. W., A. K. Webb, K. V. Rosenberg, R. D. Ohmart and B. W. Anderson. 1981. Avian censusing with the strip method: a computer simulation. Pp. 445–449 *in* Estimating numbers of terrestrial birds (C. J. Ralph and J. M. Scott, eds.). Stud. Avian Biol., No. 6.

Feist, F. G. 1972. Breeding bird populations on a sagebrush-grassland habitat in central Montana. Audubon Field Notes 22:691–695.

Fretwell, S. D. 1972. Populations in a seasonal environment. Monogr. Pop. Biol. No. 5. Princeton Univ. Press, Princeton, New Jersey.

——— and H. L. Lucas, Jr. 1969. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheor. 19:16–36.

Goss, N. S. 1881. Bell's Finch (*Poospiza belli nevadensis*) in New Mexico. Bull. Nutt. Ornithol. Club 6:116–117.

Green, R. H. 1979. Sampling design and statistical methods for environmental biologists. J. Wiley and Sons, New York, New York.

Linsdale, J. M. 1938. Environmental responses of birds in the Great Basin. Am. Midl. Nat. 19:1–206.

MacArthur, R. H. and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594–598.

Miller, A. H. 1968. Northern Sage Sparrow. Pp. 1004–1013 *in* Life histories of North American cardinals, grosbeaks, buntings, towhees, sparrows, and allies (O. L. Austin, ed.). Smithson. Inst., Washington, D.C.

Rich, T. 1980. Territorial behavior of the Sage Sparrow: spatial and random aspects. Wilson Bull. 92:425–438.

Rotenberry, J. T. and J. A. Wiens. 1978. Nongame bird communities in northwestern rangelands. USDA For. Serv. Gen. Tech. Rept. PNW–64:32–46.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco, California.

van Rossem, A. J. 1911. Winter birds of the Salton Sea region. Condor 13:129–137.

Wiens, J. A. and J. T. Rotenberry. 1979. Diet niche relationships among North American grassland and shrubsteppe birds. Oecologia 42:253–292.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.

DEPT. ZOOLOGY AND THE CENTER FOR ENVIRONMENTAL STUDIES, ARIZONA STATE UNIV., TEMPE, ARIZONA 85287. ACCEPTED 1 DEC. 1981.

Wilson Bull., 94(2), 1982, pp. 139–155

ECOLOGICAL RELEASE AND ECOLOGICAL FLEXIBILITY IN HABITAT USE AND FORAGING OF AN INSULAR AVIFAUNA

Monique I. Vassallo and Jake C. Rice

The species-poor conditions on islands (MacArthur and Wilson 1963, 1967; MacArthur 1972) are often accompanied by a number of differences in the ecology of insular populations, relative to the ecology of the same species in the mainland source population. Schoener (1965) referred to the broadening of one or more ecological parameters of a population on an island as ecological release. In such release the island population may occupy a wider range of elevations (Diamond 1970a), or more vegetation types (Diamond 1970a, Terborgh and Faaborg 1973, Yeaton and Cody 1974) than mainland counterparts; or may forage with a different, usually broader, range of positions and activities (Cody and Cody 1972, MacArthur et al. 1972, Yeaton and Cody 1974).

The ecological changes are generally explicitly or implicitly attributed to the rarefied competitive environment on the islands, especially in the absence of close taxonomic or ecological relatives, as is implied in the term "release" (Schoener 1965, Cody 1974). However, ecological differences are not always found, even when depauperate insular conditions clearly occur (Diamond 1970b, 1973, 1975; Morse 1971; Simberloff 1974). Furthermore, the ecological change need not be a niche expansion but simply a shift from one pattern of activities to another of equivalent or lesser breadth.

Taxa and guilds have been found to differ in both colonization ability and extent of ecological differences between insular and mainland populations (Morse 1971, 1977; Terborgh et al. 1978). Especially if the good colonists are also ecological generalists (Diamond 1975), insular differences in the ecology of a population may be a response to different available habitats on the island (Power 1976), rather than altered competitive interactions with the other insular populations. Evolutionary processes may, of course, produce similar habitat-related changes in the ecology of insular populations of highly specialized species, but probably over a much longer time period.

STUDY SITE AND METHODS

Gull Island is a small (0.95 km^2) island, 3 km offshore from the coast of Witless Bay, Avalon Peninsula, Newfoundland. It supports a depauperate passerine avifauna, relative to adjacent coastal areas, with species richness of about 60% that of South Head, Witless Bay

(Haycock 1973, Vassallo and Rice 1981). To determine the form and extent of the ecological differences between South Head and Gull Island, we examined the habitat use and foraging of four passerine species present in one or both sites. At least two kinds of differences may exist. Differences between sites may reflect differences in habitats available to the species, or they could be cases of ecological release, with the insular population expanding into habitats or foraging areas used on the mainland by populations of species missing on the island. We tried to separate these two evolutionarily different factors when interpreting differences between our populations.

Because of the clear difference in competitive environment, and several comparable studies of foraging in parids (Gibb 1954, Dixon 1961, Smith 1967, Sturman 1968, Krebs et al. 1972, Partridge 1976, Alerstam and Ulfstrand 1977, Morse 1978), we compared attributes of the foraging of Boreal (*Parus hudsonicus*) and Black-capped chickadee (*P. atricapillus*) populations at South Head to the foraging of Boreal Chickadees on Gull Island. The Black-capped Chickadee was absent on the island (Vassallo and Rice 1981). This seemed a particularly clear opportunity for evaluation of the relative importance of resource shifts vs ecological release in insular ecology.

We studied habitat use of Northern Waterthrushes (*Seiurus noveboracensis*), Fox Sparrows (*Passerella iliaca*), Boreal and Black-capped chickadees. The differences in competitive regimes of the insular populations of Northern Waterthrushes and Fox Sparrows were not as obvious as the absence of the congener of the Boreal Chickadee. Golden-crowned Kinglets (*Regulus satrapa*), Northern Parula (*Parula americana*) and Wilson's warblers (*Wilsonia pusilla*) were present at South Head and absent from Gull Island, as were Dark-eyed Juncos (*Junco hyemalis*), White-throated (*Zonotrichia albicollis*), Swamp (*Melospiza georgiana*), and Savannah sparrows (*Passerculus sandwichensis*) present at South Head.

Habitat measures.—The location and general description of the study areas are presented in Vassallo and Rice (1981). During regular morning censuses, singing perches of individuals of the four species were recorded, as were foraging sites for the chickadees. The census records were used to assure that only one plot per individual was included in the habitat measurements (James 1971). Individual plots were measured according to the procedure described in James (1971) and James and Shugart (1970). Tree species and diameter at breast height of each tree (dbh > 2.4 cm) within a circle of 0.04 ha were recorded. Shrub density was determined by counting all shrubs encountered on two arm-width transects at right angles to each other, crossing the center of the plot and covering 33.5 m^2. Shrubs were identified to species when recorded. An ocular tube (James and Shugart 1970) was used to take 20 + or − readings for canopy and ground cover within each plot. Presence or absence of open water (stream or pond) was recorded at each plot for the Northern Waterthrush samples. Other details were as in James and Shugart (1970).

The number of 0.04-ha samples taken per bird species per site depended on the habitat variability. Additional samples per population were included until consecutive estimates of tree density per plot differed by fewer than 25 trees (James and Shugart 1970). We took six plots for the Gull Island Fox Sparrow population, eight for the Gull Island Boreal Chickadee and nine for the South Head Black-capped Chickadee populations, and seven for all other cases.

A balanced stratified random sampling procedure was used for each species at each site. The stratified design was chosen to insure that samples were drawn equally from each section of both the island and mainland study areas. On Gull Island the presence of numerous Common Puffins (*Fratercula arctica*) reduced the availability of grassy areas for passerines. Therefore, meadows were not included in habitat analyses of either site. Otherwise, when samples were pooled across species, the sampling procedure gave representative samples of all habitats available at each site.

Habitat analyses.—We examined two questions with our habitat analyses. Were there differences in habitat use between mainland and island populations of the bird species? If so, are the "niche shifts" responses to differing habitat characteristics of the two areas, or are they responses to differences in the species composition of the avian communities of the two sites?

The tree or shrub data were converted into proportional occurrences per plot by tree species and diameter breast height. Tree and shrub data matrices were then constructed, rows being tree, shrub or dbh category and columns being the 51 plots. An arcsin transformation was performed on all the proportions (Sokal and Rohlf 1969), and the principal components of each matrix were extracted (Cooley and Lohnes 1971, James 1971). The factor scores for each plot represented the location of each plot on the ecological continua represented by several components. Because the components are orthogonal, a t-test was performed on each component to compare the factor scores of all Gull Island plots to the scores of all South Head plots. When the t-test was significant, Gull Island and South Head differed in the occurrence of the habitats ordinated along the gradient being considered. When the t-test was not significant, the habitat gradient was considered to be comparably represented at both sites.

For factors where the two sites were not different in the first analysis, a t-test of the factor scores of island and South Head plots tested whether the species being tested used equivalent parts of the habitat gradient. For habitats differentially represented at the two sites, an additional test was required. A simple t-test of factor scores would test for differences in habitat use between populations, but could not differentiate ecological release from responses of the island population to habitat characteristics different from the mainland. The mean and standard deviation of each population were calculated, and the individual factor scores were normalized by conversion to z-scores. T-tests of the z-scores by species then tested whether or not each species was using the same relative position on the habitat gradient at each site, whereas the initial t-test had tested whether the populations were occupying the same absolute position on the gradient.

Log_{10} of total tree and shrub densities were compared for each species with a t-test and a test for equality of variance (Sokal and Rohlf 1969) to look at island-mainland differences in the preference for, and breadth of, vegetation densities. Canopy and ground cover counts were compared with a Kruskal-Wallis test (Sokal and Rohlf 1969). Means and 95% confidence intervals for maximum tree heights were compared to determine overlap of habitats used by the populations, and tests of equality of variances were done to compare niche breadth between insular and mainland populations.

Foraging activities of chickadees.—Foraging activity was recorded as the frequency of use of different microhabitat positions, using the stopwatch and tape recorded procedure of Cody (1974). Six height classes were used—0.03 m (litter & ground shrubbery), 0.3–1.5 m (low shrub layer), 1.5–3.0 m, 3.0–6.1 m, >6.1 m. Three classes of vegetation were used (1) live deciduous vegetation, (2) live conifer vegetation and (3) nongreen (dead or dying leaves and needles) vegetation and dead trees or limbs. Conifers were subdivided into trunk, center, middle, and periphery, after MacArthur (1958). Data recorded were cumulative seconds an individual spent in each category.

For each of the foraging positions of the chickadees, three comparisons were made. Within populations, data collected from 1–20 June were compared to those collected from 21 June–21 July. For each period, foraging locations of Gull Island and South Head Boreal Chickadees were compared, and locations of Boreal Chickadees at South Head were compared to those of Black-capped Chickadees. Finally, the data were pooled, despite seasonal changes, to examine the most robust differences between the populations. In all cases, the G-test for independence of occurrence of discrete events was used (Sokal and Rohlf 1969).

RESULTS

Tree use between sites.—The first two components emphasized structural characteristics of the habitats. Component one was bipolar, ordinating sites from those with predominately small trees with dense, low foliage (mostly balsam fir), to areas supporting predominately trees of large dbh, where dead trees and dense canopy vegetation were common. The second component ordinated plots by increasing density of trees with densest foliage at intermediate layers of the forest, usually white spruce (Table 1). Three other components ordinated plots by increasing densities of tree species, emphasizing respectively, second growth deciduous trees such as mountain ash and mountain maple, black spruce and white birch. Because recent studies have indicated that taxonomic composition, as well as structural characteristics of the vegetation can affect bird species occurrences (Rice et al. 1981, Wiens and Rotenberry 1981), all five components were investigated to insure that subtle patterns of habitat use were not overlooked.

TABLE 1

VARIABLE WEIGHTS FOR VARIMAX ROTATED PRINCIPAL COMPONENTS OF THE TREE COMPOSITION AND STRUCTURE DATA FOR GULL ISLAND AND SOUTH HEAD PLOTS

Variable	Principal component weights				
PC	1	2	3	4	5
Trees 2.5–7.6 cm dbh	−0.805	−0.482	0.072	0.208	−0.043
Trees 7.6–12.7 cm dbh	−0.064	0.803	−0.333	−0.076	0.091
Trees 12.7–17.8 cm dbh	0.617	0.583	−0.143	−0.009	−0.066
Trees 17.8–25.4 cm dbh	0.870	0.050	−0.026	−0.107	0.132
Trees 25.4–30.0 cm dbh	0.641	−0.214	0.102	−0.166	−0.097
Trees 30.0 cm dbh	0.553	−0.343	0.320	−0.346	0.106
Balsam fir (*Abies balsamea*)	−0.831	0.124	−0.300	−0.080	−0.324
Dead trees	0.812	−0.035	−0.046	−0.395	0.115
White spruce (*Picea glauca*)	−0.023	0.680	0.031	−0.034	−0.128
White birch (*Betula papyrifera*)	0.395	−0.365	−0.301	0.060	0.903
Black spruce (*Picea mariana*)	−0.134	−0.157	−0.016	0.855	0.047
Mountain ash (*Sorbus americana*)	0.173	−0.343	0.574	0.029	0.228
Mountain alder (*Alnus crispa*)	−0.176	−0.000	0.027	0.848	−0.081
Mountain maple (*Acer spicatum*)	0.160	−0.252	0.827	−0.250	−0.079
Juneberry (*Amelanchier bartramiana*)	−0.111	0.160	0.714	0.159	−0.362
Percent variance explained	30.9	18.7	9.8	8.8	6.5

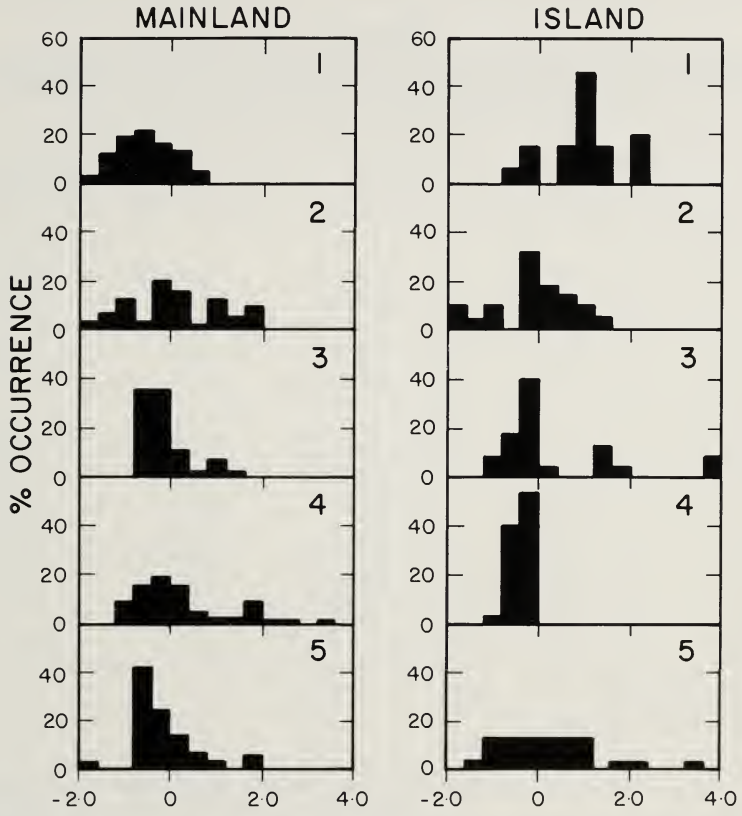


FIG. 1. Histograms of occurrences of plots from South Head (mainland plots) and Gull Island (island plots) on the five principal components from analysis of tree species composition and vegetation structure; x axis is principal component score. Numbers 1–5 refer to specific components.

Plots of habitats characterized by components 2, 3 and 5 were equally represented at Gull Island and South Head (t = 0.95, 1.32 and 1.46 [for components 2, 3 and 5, respectively]; df = 49; $P > 0.05$; Fig. 1). On component 1, South Head plots had significantly lower factor scores than did Gull Island plots, indicating denser understory vegetation, more balsam fir, and fewer large or dead trees (t = 7.71, df = 49, $P < 0.001$). Scores on component 4 were also significantly different (t = 3.33, df = 49, $P < 0.01$). Fig. 1 illustrates that although most plots at both sites supported low to intermediate densities of black spruce and/or mountain alder, at South Head a few plots had exceptionally high densities of these trees.

TABLE 2

VALUES OF *t* FOR COMPARISONS OF FACTOR SCORES FROM PRINCIPAL COMPONENT ANALYSES OF TREE AND SHRUB COMPOSITION BETWEEN POPULATIONS OF BIRDS ON SOUTH HEAD, WITLESS BAY, AND GULL ISLAND, 1977

Factor	Northern Waterthrush	Fox Sparrow	Boreal Chickadee	Boreal Chickadee (S)[a] Black-capped Chickadee (S)
Tree analysis				
1	5.07**	5.55**	1.40	0.291
2	1.08	0.202	2.04	0.373
3	0.237	1.53	0.541	1.26
4	1.51	1.58	3.10*	0.255
5	0.178	0.884	2.14	1.49
Shrub analysis				
1	1.37	2.90*	1.91	0.440
2	1.39	0.975	0.149	0.004
3	1.62	0.541	1.56	0.805
4	0.577	1.51	0.733	0.794
5	1.31	4.20**	0.383	0.985
6	0.851	0.337	0.437	0.234
7	1.37	0.0426	0.778	0.193
df =	12	11	14	13

* $P < 0.05$ (2-tailed *t*-test).
** $P < 0.01$ (2-tailed *t*-test).
[a] (S) for South Head populations only.

When the habitats on the samples from the four species are compared using these factor scores, several differences are found (Table 2). The Gull Island populations of both the Northern Waterthrush and Fox Sparrow differ significantly from the South Head populations on component 1; the Boreal Chickadee populations differ significantly on component 4. However, the two South Head chickadee populations do not differ in habitat use.

Because all significant differences in factor scores were for habitat attributes that differed between sites, the *z*-transformations and subsequent tests were necessary to determine what ecological differences existed. For each species the distribution of the populations relative to the available habitats did not differ significantly (Fox Sparrow: $t = 0.86$, df = 11, NS; Northern Waterthrush: $t = 1.31$, df = 12, NS; Boreal Chickadee: $t = 0.26$, df = 14, NS). Thus, the differences in habitat use between South Head and Gull Island populations reflect responses to differences in the range of habitats rather than competitively based ecological displacements.

When total tree densities were compared by *t*-test, no differences were

TABLE 3

DESCRIPTIVE STATISTICS AND COMPARISONS BETWEEN POPULATIONS FOR TREE AND SHRUB DENSITIES ON PLOTS USED BY FOUR PASSERINE SPECIES AT SOUTH HEAD, WITLESS BAY, AND GULL ISLAND, 1977

	South Head		Gull Island	
	$\bar{x}$	± SD	$\bar{x}$	± SD
Tree density				
Northern Waterthrush	99.9	27.7	90.1	27.6
	0.713[a]	0.001[b]	—	—
Fox Sparrow	59.7	10.5	93.9	65.3
	1.18	7.88*	—	—
Boreal Chickadee	124	71.0	100	21.3
	0.531	4.01*	—	—
Black-capped Chickadee	123	39.5	—	—
	1.09	2.10	(compared to South Head Boreal Chickadee)	
Shrub density				
Northern Waterthrush	52.0	16.6	13.6	14.2
	3.06*	0.124	—	—
Fox Sparrow	53.6	12.8	30.7	9.62
	3.11*	0.401	—	—
Boreal Chickadee	46.7	21.5	20.1	12.4
	2.62*	0.820	—	—
Black-capped Chickadee	42.3	13.7	—	—
	2.16	0.564	—	—

[a] t values for tests of equality of means, unequal variances assumed.
[b] Chi-square value for test of homogeneity of two variances.
* $P < 0.05$.

found for any of the species (Table 3). The variances were significantly different for both the Fox Sparrow and Boreal Chickadee, the former more generalized on South Head and the latter more so on Gull Island.

Shrub use between sites.—Because of the significant differences between sites on component 1 of the tree analysis emphasizing understory vegetation, we looked in detail at the shrub composition of the vegetation at the sites. Little systematic structure was apparent in the vegetation at this level, with seven eigenvalues greater than 1.0 in the principal component analysis of the shrub vegetation (Table 4). Components 2 and 4 were bipolar, whereas all others ordinated density variation in one or two shrub species. Sites on Gull Island were distributed differently from those at South Head on components 1, 3 and 5 ($t = 4.18$, $P < 0.001$; $t = 2.15$, $P < 0.05$; $t = 3.18$, $P < 0.02$; respectively, all df = 49). Other gradients in shrub composition were equally represented at both localities (Fig. 2).

When positions of the four species on these components were compared,

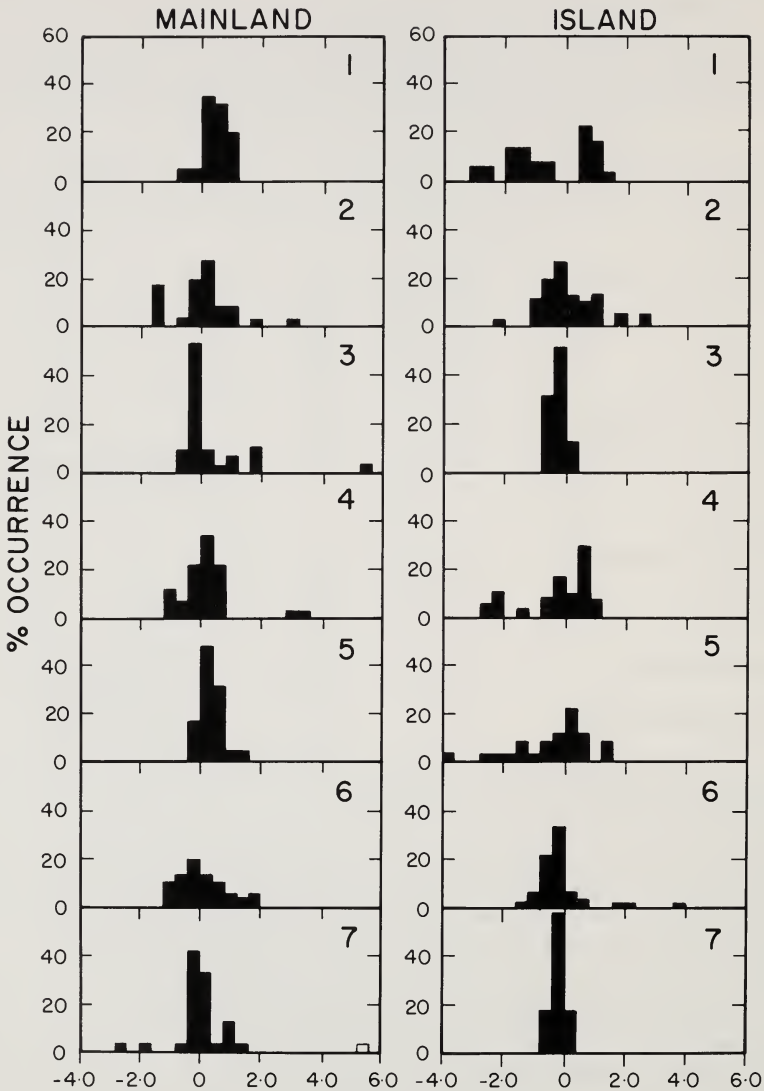


FIG. 2. Histograms of occurrences of plots from South Head and Gull Island on the seven principal components from analysis of shrub composition of the vegetation. Axes and symbols as in Fig. 1.

only the Fox Sparrow populations showed significant differences on components 1 and 5 (Table 2). Because both of these habitat gradients were differentially represented in the two areas, the relative positions of the populations were again tested by analysis of *z*-scores. No difference be-

TABLE 4

VARIABLE WEIGHTS FOR VARIMAX ROTATED PRINCIPAL COMPONENTS OF THE SHRUB COMPOSITION DATA FOR GULL ISLAND AND SOUTH HEAD PLOTS

Variable	Principal component weights						
PC	1	2	3	4	5	6	7
Balsam fir	0.244	0.880	−0.043	−0.020	0.031	0.056	0.060
Mountain alder	0.490	−0.327	0.030	0.434	0.464	−0.147	0.134
Dead shrubs	0.010	0.099	0.011	−0.676	0.381	−0.288	−0.173
Wild raisin (*Viburnum cassinoides*)	0.368	−0.605	0.116	0.102	0.094	0.386	0.001
Juneberry	−0.023	−0.030	0.070	0.048	0.085	0.874	0.053
White birch	0.079	0.046	0.016	−0.005	−0.860	−0.120	−0.058
Mountain ash	−0.855	−0.039	0.052	0.007	0.160	0.021	−0.045
White spruce	0.312	0.254	−0.184	−0.606	−0.093	0.155	−0.211
Black spruce	0.139	−0.075	0.837	0.027	0.029	−0.119	0.109
Mountain maple	−0.601	−0.270	−0.235	0.157	−0.443	−0.053	−0.047
Pin cherry (*Prunus pensylvanica*)	0.094	0.075	−0.025	0.102	0.089	0.068	0.874
Mountain holly (*Nemopanthus mucronata*)	−0.115	−0.025	0.789	0.002	−0.011	0.254	−0.127
Mixed other uncommon species	0.163	0.238	−0.117	0.626	0.205	0.068	−0.448
Percent variance explained	16.2	14.6	10.8	9.1	8.4	7.9	7.7

Table 5

Kruskal-Wallis H-values from Comparisons of Canopy and Ground Cover Counts at South Head and Gull Island for Four Passerine Species

Species	Canopy cover	Ground cover
Northern Waterthrush	1.99	9.49*
Fox Sparrow	7.44*	3.48
Boreal Chickadee	0.07	1.05
Boreal Chickadee (S)[a] vs Black-capped Chickadee	0.48	3.69

* $P < 0.01$, 2-tailed comparison.
[a] (S) is South Head only.

tween populations was found for component 1 ($t = 0.79$, df = 11), but on component 5 a barely significant difference appeared ($t = 2.32$, df = 11, $0.04 < P < 0.05$). On Gull Island the Fox Sparrow was using areas with relatively high white birch densities, whereas on South Head it was using areas with relatively low densities of this tree. This may represent a shift in the relative position of the Fox Sparrow in an insular avian community.

When total shrub densities are compared, all three species occupy habitats with significantly higher shrub densities on South Head than on Gull

Table 6

Summary of Comparisons of Attributes of Habitats of Four Passerine Species on South Head, Witless Bay, and Gull Island

	Fox Sparrow[a]	Northern Waterthrush[a]	Boreal Chickadee[a]	Boreal Chickadee[b] vs Black-capped Chickadee
Tree density	−[c]	−	−	−
Tree density variance	+[d]	−	+	−
Tree composition	+	+	+	−
Shrub density	+	+	+	−
Shrub density variance	−	−	−	−
Shrub composition	+	−	−	−
Canopy cover	+	−	−	−
Ground cover	−	+	−	−
Maximum tree height	−	−	−	−
Maximum tree height variance	+	−	−	−
Presence of water		+		

[a] Comparison of South Head and Gull Island populations.
[b] Comparison of the two South Head populations.
[c] Minus means that the comparison was not significant.
[d] Plus means that the test was significant. Specific tests are presented in Tables 2, 3 and 5, and the text.

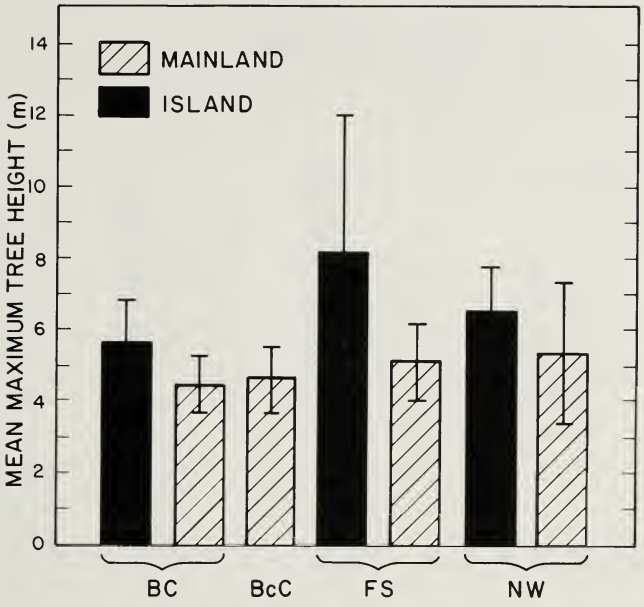


FIG. 3. Means and two standard deviations for maximum tree height on plots of each of the populations studied. BC = Boreal Chickadee, BcC = Black-capped Chickadee, FS = Fox Sparrow, NW = Northern Waterthrush, Mainland = South Head, Island = Gull Island.

Island (Table 3). However, the shrub density on South Head is greater than on Gull Island by an amount comparable to the between-population differences. Again, these differences reflect differences in available habitat rather than competitive interactions between species. The Boreal and Black-capped chickadee habitats did not differ in shrub composition or density at South Head.

Other habitat attributes.—The canopy cover differed between Gull Island and South Head only on plots of the Fox Sparrow (Table 5); the areas used on Gull Island were significantly more open. Only the Northern Waterthrush occupied areas with significantly greater ground cover on South Head than on Gull Island. No populations differed in mean canopy height, but the variance of canopy height on the Fox Sparrow sample from Gull Island was significantly greater than on South Head ($\chi^2 = 5.94$, df = 1, $P < 0.025$, Fig. 3). Finally, at South Head all seven waterthrush plots had open water present, as is characteristic of the species (Bent 1953), whereas, on Gull Island only 1 of 7 plots had open water present. Table 6 summarizes all the habitat analyses between South Head and Gull Island populations.

Chickadee foraging.—Differences in foraging location were found be-

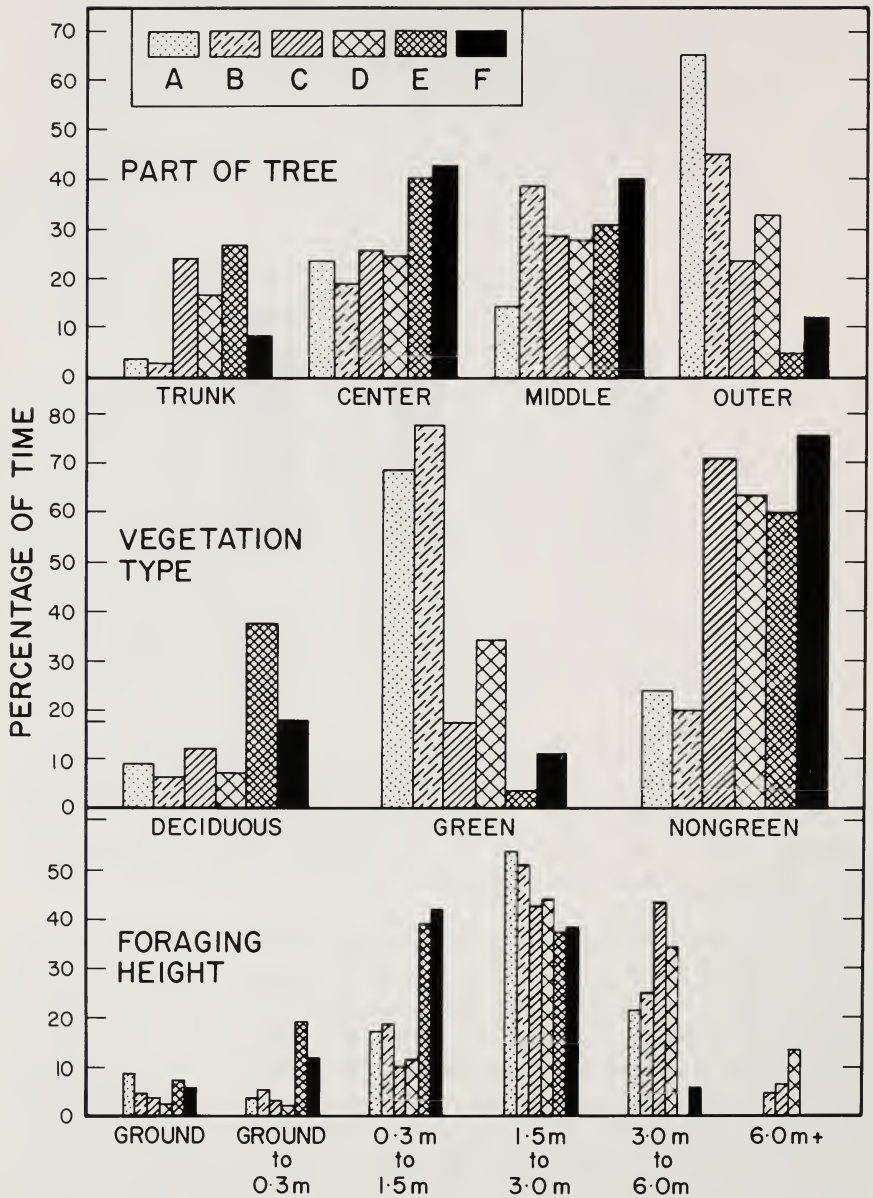


FIG. 4. Proportion of time spent foraging in each category by each chickadee population during early and late seasonal intervals. A = South Head Boreal Chickadees until June 20; B = South Head Boreal Chickadees after June 20; C = Gull Island Boreal Chickadees until June 20; D = Gull Island Boreal Chickadees after June 20; E = South Head Black-capped Chickadees until June 20; F = South Head Black-capped Chickadees after June 20.

TABLE 7

VALUES OF STATISTICS FOR G-TESTS OF THE FORAGING POSITION DATA IN FIG. 3, FOR EARLY VS LATE COMPARISONS OF EACH CHICKADEE POPULATION, AND BETWEEN POPULATIONS WITHIN EACH PERIOD

	Boreal Chickadee		Black-capped Chickadee
Early vs late	South Head	Gull Island	South Head
Foraging height	110.4	1838.6	47.9
Vegetation type	14.3	1885.8	76.7
Part of tree	135.7	36.5	71.0
Total seconds	2632	3732	3422

	Boreal Chickadee		Boreal Chickadee vs Black-capped Chickadee	
	South Head vs Gull Island		South Head	
Between populations	Early	Late	Early	Late
Foraging height	310.0	2159.3	297.7	877.1
Vegetation type	687.7	837.9	525.2	5989.9
Part of tree	396.5	37.5	260.8	757.3

All $P < 0.005$.

tween months for each chickadee sample, between Gull Island and South Head Boreal Chickadee populations, and between the two species at South Head (Table 7, Fig. 4). From early June to late June–early July each population tended to increase use of high parts of trees. Foraging decreased on deciduous trees and increased on green vegetation for all groups. Both Boreal Chickadee populations decreased use of nongreen vegetation, whereas blackcaps increased use of those areas. Island Boreal Chickadees tended to forage more towards the outer ends of branches and less on trunks later in the season, whereas South Head Boreal Chickadees decreased use of both of those areas, and increased the use of middle sections of trees.

Despite the extensive seasonal changes, significant differences were consistently present between populations. Boreal Chickadees on Gull Island foraged significantly higher in trees than either South Head group, and South Head Boreal Chickadees foraged significantly higher than did Black-capped Chickadees. Taller trees on Gull Island might account for some of this difference (Fig. 3). Both Gull Island Boreal and Black-capped chickadees foraged mainly in nongreen vegetation, whereas South Head Boreal Chickadees foraged largely in green vegetation. On South Head the two species partitioned the trees, with Boreal Chickadees using outer sections and blackcaps using inner sections. On Gull Island the Boreal Chickadees used all sections of the trees fairly evenly.

DISCUSSION

For each of the species examined, some differences in habitat use between mainland and island populations were found: the Fox Sparrow populations differed most, then the Northern Waterthrushes, and the Boreal Chickadees least. With one exception the differences in habitat use are reflections of differences in available habitat. Aside from the increase in use of white birch by Gull Island Fox Sparrows, explanations of mainland-island differences do not require additional consideration of changes in competitive interactions among species. Other insular differences from mainland populations also reflect ecological flexibility: insular Fox Sparrows increased variance in tree densities and heights used, insular Boreal Chickadees used a wider range of tree densities and waterthrushes resided in areas lacking open water.

Partitioning of foraging microhabitat by the two species of chickadees was found at South Head, consistent with the findings of previous workers on foraging of *Parus* species (Smith 1967, Sturman 1968, Partridge 1976, Morse 1978). Boreal Chickadees on Gull Island increased their use of inner parts of trees, bare branches and deciduous vegetation, areas used on South Head by Black-capped Chickadees. Corresponding to this increase in foraging microhabitat breadth, the island Boreal Chickadee density equalled or exceeded the combined density of both chickadees on South Head (Vassallo and Rice 1981).

Seasonally, similar trends were seen in the foraging activities of all populations. Perhaps these similar trends are responses to changing food availability as the season progressed. The flexibility in foraging location necessary to exploit seasonally varying food supplies may account for the greater ecological release found in the chickadees' foraging microhabitats than in the macrohabitat-use patterns of the species considered. Further, the two South Head chickadee populations showed several differences in seasonal foraging trends, such as the decreased use of nongreen vegetation by Boreal Chickadees, and the increased use of the same areas by blackcaps. These trends are consistent with the interpretation that competitive factors greatly affect foraging activities (Cody 1974).

Our findings are consistent with the literature documenting ecological shifts between mainland and island populations of many species, as cited in the introduction. Consistent with theory (Schoener 1965, MacArthur and Wilson 1967, many others) many changes, such as increased variance in several measures, indicate niche expansion of insular populations. However, for other ecological differences, including changes in species composition of habitats used and foraging heights, invoking changes in competition as explanation for the differences is unnecessary.

A number of studies have argued that species which are particularly

good colonists are often ecological generalists (Simberloff and Wilson 1969, 1970; Diamond 1975; Terborgh et al. 1978). Our findings are consistent with that proposal. For species showing ecological flexibility we found competition may not be necessary to explain even large differences between mainland and insular populations. If available island habitats differ from adjacent mainland areas, their use by populations of a particular species could differ greatly. Nonetheless, the populations in question could be filling the same relative role or guild in both communities, and be optimizing use of available habitat. However, a species occupying habitats similar in absolute properties could in fact be playing very different roles in the insular and mainland communities.

In our study, it appears that microhabitat foraging positions are more likely to show direct effects from changes in competitive pressures, although it was not possible to document the extent of insular differences in available prey. Our conclusion is inferred from the increased use by insular Boreal Chickadees of areas used on South Head by Black-capped Chickadees. Such flexibility in foraging location has been found in other studies of parids (Krebs et al. 1972, Partridge 1976). Flexibility in microhabitat use should be common to enable foraging activities to respond to seasonal variation in resources. Consequently, for insular populations of birds, microhabitats used for foraging activities may be preadapted to show a faster and greater response to changing competitive regimes than do macrohabitat preferences. Careful comparisons of both habitats and foraging resources available, as well as those used, are necessary to distinguish the effects of competition and simple ecological flexibility on insular community dynamics.

SUMMARY

Aspects of macrohabitat use by Fox Sparrows (*Passerella iliaca*), Northern Waterthrushes (*Seiurus noveboracensis*) and Boreal Chickadees (*Parus hudsonicus*) differ between insular Newfoundland and coastal populations of each species. The differences generally reflected changes in the ranges of available habitats between localities, rather than responses to differing competitive environments. Foraging locations of coastal and insular Boreal Chickadee populations were also compared. Differences were found—the Boreal Chickadee expanded the breadth of its foraging activities to include areas used on the mainland by Black-capped Chickadees (*P. atricapillus*), a species absent on the island. Seasonal differences were also found in chickadee foraging behavior at both sites. Niche partitioning between the two mainland species of chickadees was accomplished via differences in foraging position rather than macrohabitat differences.

ACKNOWLEDGMENTS

Parts of this work were included in the M.Sc. thesis presented by the first author to the graduate school of Memorial University of Newfoundland. Financial support by the graduate school to the first author and by the National Research Council of Canada to the second

author is gratefully acknowledged. The support and assistance of L. Vassallo is also appreciated. Two anonymous reviewers provided useful suggestions for improvements to the manuscript.

LITERATURE CITED

ALERSTAM, T. AND S. ULFSTRAND. 1977. Niches of tits *Parus* in two types of African woodland. Ibis 119:521–524.

BENT, A. C. 1953. Life histories of North American Wood Warblers. Natl. Mus. Bull. 203.

CODY, M. L. 1974. Competition and the structure of bird communities. Monogr. Pop. Biol. 5. Princeton Univ. Press, Princeton, New Jersey.

——— AND B. B. J. CODY. 1972. Territory size, food density and clutch size in island wren populations. Condor 75:473–477.

COOLEY, W. W. AND P. R. LOHNES. 1971. Multivariate data analysis. John Wiley & Sons, New York, New York.

DIAMOND, J. M. 1970a. Ecological consequences of island colonization by southwest Pacific birds. I. Types of niche shifts. Proc. Natl. Acad. Sci. 67:529–536.

———. 1970b. Ecological consequences of island colonization by southwest Pacific birds. II. The effect of species diversity on total population density. Proc. Natl. Acad. Sci. 67:1715–1721.

———. 1973. Distributional ecology of New Guinea birds. Science 179:759–769.

———. 1975. Assembly of species communities. Pp. 342–444 *in* Ecology and evolution of communities (M. L. Cody and J. M. Diamond, eds.). Belknap, Cambridge, Massachusetts.

DIXON, K. L. 1961. Habitat distribution and niche relationships in North American species of *Parus*. Pp. 179–216 *in* Vertebrate speciation (W. F. Blair, ed.). Univ. Texas Press, Austin, Texas.

GIBB, J. 1954. Feeding ecology of tits, with notes on the Tree Creeper and Goldcrest. Ibis 96:513–543.

HAYCOCK, K. A. 1973. Ecological studies on Gull Island, Witless Bay, with particular reference to the avifauna. M.Sc. thesis, Memorial Univ. Newfoundland, St. John's, Newfoundland.

JAMES, F. C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bull. 83:215–236.

——— AND H. H. SHUGART. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727–736.

KREBS, J. R., M. MACROBERTS AND J. M. CULLEN. 1972. Flocking and feeding in the Great Tit, *Parus major*—an experimental study. Ibis 114:507–530.

MACARTHUR, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology 39:599–619.

———. 1972. Geographical ecology. Harper and Row, New York, New York.

———, J. M. DIAMOND AND J. R. KARR. 1972. Density compensation in island faunas. Ecology 53:330–342.

——— AND E. O. WILSON. 1963. An equilibrium theory of insular zoogeography. Evolution 17:373–387.

——— AND ———. 1967. The theory of island biogeography. Monogr. Pop. Biol. 1. Princeton Univ. Press, Princeton, New Jersey.

MORSE, D. H. 1971. The foraging of warblers isolated on small islands. Ecology 52:216–228.

———. 1977. The occupation of small islands by passerine birds. Condor 79:399–412.

———. 1978. Structure and foraging patterns of flocks of tits and associated species in an English woodland. Ibis 120:298–312.

Partridge, L. 1976. Field and laboratory observations on the foraging and feeding techniques of Blue Tits (*Parus caeruleus*) and Coal Tits (*P. ater*) in relation to their habitat. Anim. Behav. 24:534–544.

Power, D. M. 1976. Avifauna richness of the California Channel Islands. Condor 78:394–398.

Rice, J., R. D. Ohmart and B. W. Anderson. 1981. Bird community use of riparian habitats: the importance of temporal scale in interpreting discriminant analysis. Pp. 186–196 *in* The use of multivariate statistics in studies of wildlife habitat (D. Capen, ed.). USDA For. Serv. Gen. Tech. Rept. RM–87.

Schoener, T. W. 1965. The evolution of bill size differences among sympatric congeneric birds. Evolution 19:189–213.

Simberloff, D. S. 1974. Equilibrium theory of island biogeography and ecology. Ann. Rev. Ecol. Syst. 5:161–182.

——— and E. O. Wilson. 1969. Experimental zoogeography of islands: the colonization of empty islands. Ecology 50:278–295.

——— and ———. 1970. Experimental zoogeography of islands: a two year record of colonization. Ecology 51:934–937.

Smith, S. M. 1967. An ecological study of winter flocks of Black-capped and Chestnut-backed chickadees. Wilson Bull. 79:200–207.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco, California.

Sturman, W. A. 1968. The foraging ecology of *Parus atricapillus* and *P. rufescens* in the breeding season, with comparisons with other species of *Parus*. Condor 70:309–322.

Terborgh, J. and J. Faaborg. 1973. Turnover and ecological release in the avifauna of Mona Island, Puerto Rico. Auk 90:759–779.

———, ——— and H. J. Brockman. 1978. Island colonization by Lesser Antillean birds. Auk 95:59–72.

Vassallo, M. I. and J. C. Rice. 1981. Differential passerine density and diversity between Newfoundland and off-shore Gull Island. Wilson Bull. 93(3):340–349.

Wiens, J. A. and J. T. Rotenberry. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecol. Monogr. 51:21–41.

Yeaton, R. I. and M. L. Cody. 1974. Competitive release in island Song Sparrow populations. Theoret. Pop. Biol. 5:42–58.

Dept. Biology, Memorial Univ. of Newfoundland, St. John's, Newfoundland A1B 2X8 Canada and Dept. Zoology, Arizona State Univ., Tempe, Arizona 85281. (Present address JCR: Center for Environmental Studies, Arizona State Univ., Tempe, Arizona 85281.) Accepted 15 June 1981.

Wilson Bull., 94(2), 1982, pp. 156–175

AVIAN NEST DENSITIES AND NEST-SITE SELECTION IN FARMSTEAD SHELTERBELTS

Richard H. Yahner

Farmstead shelterbelts are man-made habitats consisting of parallel rows of trees and shrubs designed to protect farmsteads from damaging winds, drifting snow and blowing soil, and to moderate the effects of wind, thereby reducing heat loss from humans, domestic animals, and farm buildings (Smith and Scholten 1980). These habitats may be viewed as small (generally <1 ha) "wooded islands" surrounded by extensive fields of crops, pastures and natural prairies; however, despite their small size and isolation from other wooded habitats, shelterbelts are a source of food and song perches as well as roosting and nesting sites for a number of bird species (Orendurff 1941, Martin 1978). Avian communities in shelterbelts have been examined during the breeding season (Weiser and Hlavinka 1956; Cassel et al. 1966, 1967; Emmerich 1978; Martin 1978). However, with the exception of studies dealing with Mourning Doves (*Zenaida macroura*) (see Nelson 1976 for review), Ring-necked Pheasants (*Phasianus colchicus*) (e.g., Olson and Flake 1975) and Ferruginous Hawks (*Buteo regalis*) (Lokemoen and Duebbert 1976), little is known about the nesting ecology of many bird species breeding in shelterbelts. A study by Field (1971) represents the only published report giving the total number of nests per bird species. Her study dealt only with a portion of one shelterbelt where tree/shrub species used and height above ground of 75 nests of four bird species were noted. As part of an investigation of breeding-bird diversity in 69 shelterbelts, Martin (1978) examined 185 nests of eight species and noted tree/shrub species used, height above ground, lateral distance of nest from main stem, and distance of nest from top of tree/shrub. However, his study did not attempt to locate total nests per shelterbelt nor total nests per season.

A determination of both the number of avian species nesting in farmstead shelterbelts and the abundance of nests per species is an initial and important step in assessing whether or not these small, narrow, agricultural habitats are valuable nesting areas or instead perhaps function to attract predators, hence reducing fledging success (see Gates and Gysel 1978). Moreover, because farmstead shelterbelts are restricted in size, the availability of nest-sites conceivably could be a limiting resource to birds. Thus, a knowledge of factors critical to nest-site selection would give a better understanding of how coexisting nesting species effectively exploit these "wooded islands" (after Pianka 1973, Schoener 1974).

In this paper, I examine the suitability of farmstead shelterbelts as nesting habitats for birds by estimating the annual density of total nests per bird species. Further, I quantify patterns of nest-site selection in common nesting bird species based on two components: (1) types of woody species used as nesting substrate and (2) structural characteristics of nest-sites. Results obtained by this study may provide valuable insight into avian nesting requirements so that effective procedures for future planting and maintenance of farmstead shelterbelts can be formulated to benefit nesting avifauna. Such information would be particularly helpful in the intensively-farmed areas of the Great Plains where wooded habitats are at a premium, comprising less than 3% of the total area in this region (Griffith 1976).

STUDY AREA AND METHODS

The study was conducted at the University of Minnesota's Rosemount Agricultural Experiment Station, Dakota Co., Minnesota. Seven shelterbelts were studied ranging in size from 0.21–0.79 ha and in age from 4–33 years. The number of rows of trees and shrubs per shelterbelt varied from 3–9; 30 species of coniferous and deciduous trees and shrubs were planted by landowners. Shelterbelts and land-use practices of the Experiment Station are representative of those in this agricultural region.

Active and inactive nests were located by systematically searching the ground level and all trees and shrubs in each shelterbelt; searches were conducted at least once per week from late June to late September in 1978 and from early March to late September in 1979. If eggs or young were found in a nest that was known to have been constructed earlier in the year (beginning after late March) and subsequently either abandoned or used to rear young by the same or different species, the nest was considered as another nest. Thus, a nest (or nest-site) is defined to include new nests, nests used for renesting, and those used by one species but constructed by another. Nests were often detected by observations of the activities of breeding adults.

Nests constructed prior to the 1978 breeding season were not considered in the analyses and could be distinguished easily from nests of the 1978 breeding season by degree of deterioration occurring over the previous winter. Because the study did not begin until June 1978, nearly 80% of the nests found this year were no longer in use. Species that had built nests subsequently abandoned ("inactive") were determined (estimated 95% accuracy) by the design of the nest or by the presence of shell fragments and/or feathers in the nest (Harrison 1975). The identity of nests positioned higher than 2.5 m above ground was resolved by using 7 × 35 field glasses at ground level, by climbing to the height of the nest, or by inspection with a mirror and pole device (Parker 1972). The tree and shrub used as a nesting substrate was recorded for each active and inactive nest positioned above ground level; nests on the ground were noted. In addition, 11 structural characteristics of each active and inactive nest above ground level were measured (Table 1).

Densities of nests were computed each year per individual bird species, individual shelterbelt, total bird species and total shelterbelts. I believe that virtually all nests in 1979 were located and correctly identified. However, because the 1978 search of nests began in June, an unknown fraction of the total nests constructed in 1978 likely was not found due to destruction by predators or climatic factors. Thus, a comparison of densities between 1978 and 1979 is probably not valid. There also are other problems inherent in comparisons of

Table 1

Abbreviations and Descriptions of 11 Structural Characteristics Measured at Each Active and Inactive Bird Nest Located above Ground Level in Seven Farmstead Shelterbelts in Southern Minnesota in 1978 and 1979

Abbreviation	Description
HTTR	Height (m) of tree or shrub in which the nest was located.
HTNT	Height (m) of the nest above ground.
DICA	Diameter (m) of the canopy of the tree or shrub at the height of the nest above ground.
DITR	Diameter (cm) of the largest woody stem touching and/or supporting the nest; measured at the nest-site.
DINT	Lateral distance (m) of the nest from the main trunk of the tree or shrub containing the nest.
PTGC	Percentage of herbaceous vegetation within a 1-m radius of a point directly below the nest at ground level.
HTGC	Maximum height (cm) of herbaceous vegetation within a 1-m radius of a point directly below the nest at ground level.
STLE	Number of woody stems <2.5 cm in diameter which was within a 1-m radius of the nest but exclusive of the woody stem nearest the nest (see DITR above).
STMO	Number of woody stems ≥2.5 cm in diameter which was within a 1-m radius of the nest but exclusive of the woody stem nearest the nest (see DITR above).
COMP	Compass direction (degrees) of the nest relative to the position of the main trunk of the tree or shrub containing the nest.
CLOS	Extent of closure or conspicuousness of a nest based on the amount of woody and herbaceous vegetation (estimated to the nearest 10%) in an approximate 1-m radius sphere surrounding the nest-site.

nest densities as true of most field studies (see Miller and Johnson 1978). However, I feel that a comparison of approximate densities has value when comparing among bird species or habitats if done with caution (e.g., see Gates and Gysel 1978).

Nest-site selection based on differential use of woody species by all bird species combined (N = 17) or by individual bird species (N = 5 most common bird species) was determined by comparing observed versus expected number of nests per woody species using tests for goodness of fit (Sokal and Rohlf 1969). Ratios of observed to expected numbers of nests of the five common bird species in each shrub or tree ("woody") species were used to arbitrarily rank individual nesting substrates; a ratio ≥1.50 was used to designate a woody species as a preferred substrate. Substrate nesting breadth, NB_{su}, or the degree of ecological specialization in selection of woody species for nest-sites, was derived for each of the five common bird species. NB_{su} was based on actual availability of each woody species in the seven shelterbelts and was obtained by the equation:

$$NB_{su} = (\lambda i)^{1/N_i}$$

and

$$\log \lambda_i = (\Sigma\, p_{ij} \log q_j - \Sigma\, p_{ij} \log p_{ij})(N_i).$$

For bird species i, N_i is the total number of nests, p_{ij} is the proportion of observed nests in the j^{th} woody species and q_j is the proportion of expected nests in the j^{th} woody species. Values of NB_{su} could range from 0–1, with 1 indicating maximum generality in use of different woody species as nesting substrates (see Petraitis 1979). Substrate nesting overlap, NO_{su}, was calculated between pairs of the five common bird species by the sum of the proportions of nests in common by a pair that were located in each of the woody species (modified from Yeaton 1974).

Nest-site selection based on the 11 structural characteristics of each nest-site (Table 1) was examined by stepwise discriminant analysis (BMDP7M, Dixon and Brown 1979), where $g = 5$ groups (common bird species), $P = 11$ variables (structural characteristics, Table 1), and $N = 589$ cases (total nests of the five common bird species) in the data matrix. Discriminant analysis is an appropriate multivariate statistical technique to detect differences in microhabitat use among species (see Dueser and Shugart 1978, 1979). *A priori* probability of membership for each case in a group was based on the proportion of total cases represented in that group. Normality and homogeneity of variances for the variables were ensured by appropriate transformations (Green 1979, Johnson 1981), and each were tested by graphical plots of observations or by F_{max}-tests, respectively (Sokal and Rohlf 1969, Johnson 1981). Characteristics were entered into the discriminant functions in decreasing order of their importance in discriminating nest-sites among bird species (after Raphael 1981). A characteristic was excluded from entry if the F-to-enter (statistic computed at each step from a single-classification analysis of covariance where covariates are previously entered characteristics) did not exceed the F-to-remove (statistic obtained for the characteristic using a single-classification ANOVA before entering any characteristic into the function) (Dixon and Brown 1979). An approximate F-statistic based on transformation of Wilks' Λ was used to test for overall differences among group means based on the characteristics entered into the discriminant function; F values computed from Mahalanobis D^2 statistics tested between each pair of group means (Lachenbruch 1975:25, Dixon and Brown 1979). Eigenvalues, discriminating information and group means of orthogonal canonical variables (linear combinations of structural characteristics) were derived from between-group and within-group covariance matrices. The canonical variables were adjusted so that the (pooled) within-group variances were 1 and their overall mean was 0; the canonical variables then were evaluated at group means (Dixon and Brown 1979). The significance of discrimination afforded by each of the canonical variables (discriminant functions) was tested using Bartlett's χ^2 approximation tests based on Wilks' Λ criterion computed as a function of the eigenvalues (Cooley and Lohnes 1971:249). A jackknifed validation procedure was used to reduce the bias of group classifications (each case is classified into a group based on a classification function which includes all cases except the one being classified [Dixon and Brown 1979]).

For each individual case (nest), Mahalanobis D^2 was derived as the distance to each group (species) mean. These distances were used to calculate a mean Mahalanobis D^2 for each of the five common bird species. Structural nesting breadth, NB_{st}, then was estimated by obtaining a coefficient of variation based on mean values of Mahalanobis D^2 for each of the five species (modified from Dueser and Shugart 1979). The coefficient of variation is a proper measure of variation when comparing sample means that are known to be statistically different (Sokal and Rohlf 1969) and can be an approximation of breadth in resource use when using discriminant analysis (Dueser and Shugart 1979). Structural nesting overlap, NO_{st}, of the five common bird species was determined by a plot of the two principal canonical variables (Lachenbruch 1975) and the principal axes technique (see Sokal and Rohlf 1969, Dueser and Shugart 1979, Williams 1981). A plot of 95% confidence ellipses for species' cases was made rather than a plot using ellipses for species means. NO_{st} between two species then was computed as the ratio of the area of overlap for the two species relative to the cumulative

area, for that pair of species (after Dueser and Shugart 1979). Thus, NB_{st} was obtained by simultaneously considering all canonical variables extracted, whereas NO_{st} was based only on the two canonical variables giving the most discriminating information among bird species.

RESULTS

Nest densities.—A total of 617 nests was found in seven shelterbelts; 272 (81.9 nests/ha) in 1978 and 345 (103.9 nests/ha) in 1979 (Table 2). Densities of nests among individual shelterbelts in both years averaged 88.5 nests/ha and ranged from 28.8 nests/ha in a three-row, 5-year-old coniferous shelterbelt in 1978 to 186.4 nests/ha in a five-row, 32-year-old coniferous-deciduous shelterbelt in 1979.

Nine of 17 bird species nested in the shelterbelts in both 1978 and 1979, whereas eight additional species nested in either 1978 or 1979 only (Table 2). Nests of Common Grackle (*Quiscalus quiscula*), Mourning Dove, American Robin (*Turdus migratorius*), Gray Catbird (*Dumatella carolinensis*) and Chipping Sparrow (*Spizella passerina*) comprised 95.5% (N = 589) of the total number of nests found in both years combined. Variation in density of nests among individual shelterbelts within or between years often was attributed to the presence of large numbers of grackles. For example, density of grackle nests nearly doubled from 1978 (36.4 nests/ha) to 1979 (64.5 nests/ha); nests of this species occurred in all shelterbelts in 1979 versus five of seven shelterbelts in 1978. Ring-necked Pheasant, Downy Woodpecker (*Picoides pubescens*), Barn Swallow (*Hirundo rustica*), Black-capped Chickadee (*Parus atricapillus*), American Goldfinch (*Carduelis tristis*) and Vesper Sparrow (*Pooecetes gramineus*) were observed in one or more shelterbelts during the breeding season of both years (see Yahner 1980a) but nested in other habitats at the Rosemount Station.

Selection of substrate.—A total of 3589 woody plants of 31 species was available as substrate for nests in the seven shelterbelts (Table 3). Numbers of observed nests for all bird species combined were considerably different from those expected in several abundant ($N > 30$ individual plants) coniferous and deciduous species ($P < 0.001$). Preferred coniferous species included Colorado blue spruce (*Picea pungens*), white spruce (*P. glauca*) and Black Hills spruce (*P. g. densata*), whereas infrequently used conifers were white cedar (*Thuja occidentalis*), red pine (*Pinus resinosa*) and Douglas fir (*Pseudotsuga menziesii*). Deciduous species favored for nest-sites were eastern cottonwood (*Populus deltoides*), silver maple (*Acer saccharinum*) and box elder (*A. negundo*). Fewer nests than expected were found in various deciduous trees and shrubs, such as green ash (*Fraxinus pennsylvanica*), caragana (*Caragana arborescens*) and amur maple (*A. ginnala*). In contrast, numbers of observed compared to expected nests were nearly equal in ponderosa pine (*P. ponderosa*) and tartarian

Table 2

Total Number of Nests, Proportion (%) of Total Nests and Density (no./ha) of Total Nests of 17 Bird Species in Seven Farmstead Shelterbelts (3.32 ha) in Southern Minnesota in 1978, 1979 and Both Years Combined

Bird species	Total no. nests			Proportion total nests			Density total nests		
	1978	1979	both	1978	1979	both	1978	1979	both
Common Grackle (*Quiscalus quiscula*)	121	214	335	44.5	62.0	54.3	36.4	64.5	50.5
Mourning Dove (*Zenaida macroura*)	62	74	136	22.8	21.4	22.0	18.7	22.3	20.5
American Robin (*Turdus migratorius*)	54	33	87	19.9	9.6	14.1	16.3	9.9	13.1
Gray Catbird (*Dumetella carolinensis*)	12	5	17	4.4	1.5	2.8	3.6	1.5	2.6
Chipping Sparrow (*Spizella passerina*)	8	6	14	2.9	1.7	2.3	2.4	1.8	2.1
Brown Thrasher (*Toxostoma rufum*)	1	4	5	0.4	1.2	0.8	0.3	1.2	0.8
Common Crow (*Corvus brachyrhynchos*)	4	0	4	1.5	0.0	0.6	1.2	0.0	0.6
Song Sparrow (*Melospiza melodia*)	2	2	4	0.7	0.6	0.6	0.6	0.6	0.6
Blue Jay (*Cyanocitta cristata*)	2	1	3	0.7	0.3	0.5	0.6	0.3	0.5
Red-winged Blackbird (*Agelaius phoeniceus*)	3	0	3	1.1	0.0	0.5	0.9	0.0	0.5
Eastern Kingbird (*Tyrannus tyrannus*)	1	1	2	0.4	0.3	0.3	0.3	0.3	0.3
Indigo Bunting (*Passerina cyanea*)	2	0	2	0.7	0.0	0.3	0.6	0.0	0.3
Great Horned Owl (*Bubo virginianus*)	0	1	1	0.0	0.3	0.2	0.0	0.3	0.2
Starling (*Sturnus vulgaris*)	0	1	1	0.0	0.3	0.2	0.0	0.3	0.2
Common Yellowthroat (*Geothlypis trichas*)	0	1	1	0.0	0.3	0.2	0.0	0.3	0.2
House Sparrow (*Passer domesticus*)	0	1	1	0.0	0.3	0.2	0.0	0.3	0.2
Eastern Meadowlark (*Sturnella magna*)	0	1	1	0.0	0.3	0.2	0.0	0.3	0.2
Total	272	345	617				81.9	103.9	93.4

Table 3

Abundance of and Use of 31 Woody Species as Nesting Substrate by 17 Bird Species in Seven Farmstead Shelterbelts (3.32 ha) in Southern Minnesota in 1978 and 1979

Woody species	Total no. plants	Observed no. nests	Expected no. nests[a]	Proportion total observed nests
Colorado blue spruce (*Picea pungens*)	113	125	19.4	20.3
White spruce (*Picea glauca*)	242	124	41.6	20.1
Cottonwood (*Populus deltoides*)	201	60	34.6	9.9
Silver maple (*Acer saccharinum*)	197	50	33.9	8.1
Ponderosa pine (*Pinus ponderosa*)	220	38	37.8	6.6
Box elder (*Acer negundo*)	33	35	5.7	5.7
Black Hills spruce (*Picea glauca densata*)	37	30	6.4	4.9
Green ash (*Fraxinus pennsylvanica*)	421	20	72.4	3.2
Tartarian honeysuckle (*Lonicera tatarica*)	111	19	19.1	3.1
White cedar (*Thuja occidentalis*)	195	16	33.5	2.6
Jack pine (*Pinus banksiana*)	72	14	12.4	2.3
Caragana (*Caragana arborescens*)	423	13	72.7	2.1
Amur maple (*Acer ginnala*)	153	12	26.3	1.9
Norway spruce (*Picea abies*)	88	11	15.1	1.8
Red pine (*Pinus resinosa*)	171	10	29.4	1.6
American elm (*Ulmus americana*)	112	9	19.3	1.5
Ural willow (*Salix purpurea*)	220	5	37.8	0.8
Buffalo berry (*Shepherdia argentea*)	17	4	2.9	0.6
Flowering crab (*Malus floribunda*)	7	3	1.2	0.5
Common lilac (*Syringa vulgaris*)	251	3	43.2	0.5
Russian olive (*Elaeagnus angustifolia*)	25	2	4.3	0.3
Red-berried elder (*Sambucus pubens*)[b]	10	2	1.7	0.3
High-bush cranberry (*Viburnum trilobum*)	9	2	1.5	0.3
River birch (*Betula nigra*)	1	1	0.2	0.2
Honey locust (*Gleditsia tricancanthos*)	99	1	17.0	0.2
Chokecherry (*Prunus virginiana*)	11	1	1.9	0.2
Southern arrowwood (*Viburnum dentatum*)	24	1	4.1	0.2
Gray dogwood (*Cornus racemosa*)	18	0	3.1	0.0
Red-osier dogwood (*Cornus stolonifera*)	10	0	1.7	0.0
Laurel-leaved willow (*Salix pentandra*)	9	0	1.5	0.0
Douglas fir (*Pseudotsuga menziesii*)	89	0	15.3	0.0
Miscellaneous[c]	—	6	—	1.0
Total	3589	617	—	—

[a] Expected number of nests was determined from the total number of plants and the total number of observed nests. Expected number of nests is significantly different from observed number of nests ($\chi^2 = 1227$, df = 30, $P < 0.001$. Test for goodness of fit, Sokal and Rohlf (1969).

[b] Woody species which colonized shelterbelts.

[c] Refers to nests found on ground or in log and brush piles.

Table 4

Total Number of Observed Nests (and Expected Nests) of Five Common Bird Species in 26 Woody Species Used as Nesting Substrate in Seven Farmstead Shelterbelts in Southern Minnesota in 1978 and 1979

Woody species[a]	Total number of nests/bird species[b]				
	Common Grackle	Mourning Dove	American Robin	Gray Catbird	Chipping Sparrow
Colorado blue spruce	57 (10.55)[2]	35 (4.28)[1]	25 (2.74)[2]	1 (0.54)[7]	8 (0.44)[1]
White spruce	56 (22.59)[5]	48 (9.17)[3]	19 (5.87)[6]	0 (1.15)	0 (0.94)
Cottonwood	50 (18.76)[4]	8 (7.62)	3 (4.87)	0 (0.95)	0 (0.78)
Silver maple	40 (18.39)[6]	5 (7.47)	4 (4.78)	0 (0.93)	0 (0.77)
Ponderosa pine	37 (20.53)[7]	0 (8.34)	1 (5.33)	0 (1.04)	0 (0.86)
Box elder	29 (3.08)[1]	0 (1.25)	4 (0.80)[4]	0 (0.16)	0 (0.13)
Black Hills spruce	11 (3.45)[3]	9 (1.40)[2]	8 (0.90)[3]	1 (0.18)[5]	1 (0.14)[2]
Green ash	10 (39.30)	4 (15.95)	6 (10.21)	0 (1.99)	0 (1.64)
Tartarian honeysuckle	0 (10.36)	3 (4.21)	2 (2.70)	8 (0.53)[4]	3 (0.43)[3]
White cedar	7 (18.20)	3 (7.39)	5 (4.73)	0 (0.92)	0 (0.76)
Jack pine	7 (6.72)	4 (2.73)	0 (1.75)	0 (0.34)	0 (0.28)
Caragana	12 (39.48)	0 (16.03)	0 (10.25)	0 (2.00)	0 (1.65)
Amur maple	0 (14.28)	10 (5.80)[4]	2 (3.71)	0 (0.72)	0 (0.60)
Norway spruce	4 (8.21)	0 (3.33)	4 (2.13)[7]	0 (0.42)	2 (0.34)[4]
Red pine	9 (15.96)	0 (6.48)	0 (4.15)	0 (0.81)	0 (0.67)
American elm	3 (10.45)	1 (4.24)	1 (2.71)	1 (0.53)[6]	0 (0.44)
Ural willow	0 (20.53)	2 (8.34)	0 (5.33)	0 (1.04)	0 (0.86)
Buffalo berry	0 (1.59)	1 (0.64)	0 (0.41)	2 (0.08)[2]	0 (0.07)
Flowering crab	1 (0.65)	0 (0.27)	2 (0.17)[1]	0 (0.03)	0 (0.03)
Common lilac	2 (23.42)	0 (9.51)	0 (6.08)	1 (1.19)	0 (0.98)
Russian olive	0 (2.33)	1 (0.95)	1 (0.61)	0 (0.12)	0 (0.10)
Red-berried elder	0 (0.93)	0 (0.38)	0 (0.24)	2 (0.05)[1]	0 (0.01)
High-bush cranberry	0 (0.84)	0 (0.34)	0 (0.22)	1 (0.04)[3]	0 (0.04)
River birch	0 (0.09)	1 (0.04)	0 (0.02)	0 (0.00)	0 (0.00)
Honey locust	0 (9.24)	1 (3.75)	0 (2.40)	0 (0.47)	0 (0.39)
Chokecherry	0 (1.02)	0 (0.42)	1 (0.27)[5]	0 (0.05)	0 (0.04)
No. woody species used	16	16	16	8	4
Total no. observed nests	335	136	87	17	14
G-statistics[c]	782	314	174	35	39
Level of significance	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P > 0.10$	$P > 0.01$
Substrate nesting breadth, NB_{su}[d]	0.44	0.31	0.31	0.09	0.08

[a] Scientific names of woody species and total number of individual plants for each are given in Table 3. Woody species not used by at least one of five common bird species are excluded from table.

[b] Rank of each woody species as nesting substrate per bird species is based on the ratio of observed to expected number of nests. The greater the ratio, the higher the rank as indicated by a lower numeric subscript. A ratio ≥ 1.50 arbitrarily designated a preference as a nesting substrate; a ratio <1.50 was excluded from ranking.

[c] Comparison of observed to expected numbers of nests per bird species (df = 30). Test for goodness of fit, Sokal and Rohlf (1969).

[d] See text for derivation.

TABLE 5

SUBSTRATE NESTING OVERLAP, NO_{SU}, BETWEEN PAIRS OF FIVE COMMON BIRD SPECIES NESTING IN SEVEN FARMSTEAD SHELTERBELTS IN SOUTHERN MINNESOTA IN 1978 AND 1979

Bird species pair	NO_{su} (%)[a]
Common Grackle—Mourning Dove	55
Common Grackle—American Robin	59
Common Grackle—Gray Catbird	11
Common Grackle—Chipping Sparrow	22
Mourning Dove—American Robin	78
Mourning Dove—Gray Catbird	15
Mourning Dove—Chipping Sparrow	35
American Robin—Gray Catbird	15
American Robin—Chipping Sparrow	43
Gray Catbird—Chipping Sparrow	33

[a] NO_{su} (%) is calculated as the sum of proportions of nests (Table 4) in common by a pair in each woody species used as a nesting substrate.

honeysuckle (*Lonicera tatarica*). Three of the five common nesting bird species showed a significant difference ($P < 0.001$) in observed versus expected use of nesting substrate (Table 4). All five common bird species preferred spruces (*Picea* spp.), yet each also displayed specific preferences for other woody species.

The five common bird species varied in substrate nesting breadth, NB_{su} (Table 4). NB_{su} was highest in grackles, intermediate in doves and robins, and lowest in catbirds and sparrows. The greatest amount of substrate nesting overlap, NO_{su}, occurred with doves and robins (78%, Table 5). These two species exhibited similar NO_{su} with grackles (55–59%). In contrast, catbirds had little joint use of nesting substrate with doves (15%), robins (15%) and grackles (11%). NO_{su} between sparrows and each of the four other species ranged from 22–43%.

Selection of structural characteristics.—Stepwise discriminant analysis based on 11 structural characteristics (Table 1) measured at nest-sites (N = 589) indicated that group means among the five common bird species were not equal ($F = 25.11$; df = 32, 2129; $P < 0.001$). In addition, the group mean of each bird species was significantly different from those of the other species in paired comparisons (F's = 3.73–53.78; df's = 8, 22–462; P's < 0.001). Segregation of nest-sites in discriminant space (after Dueser and Shugart 1979, Raphael 1981) was due only to 8 of 11 structural characteristics (Table 6); of the 11 characteristics, HTTR, DITR and COMP (see Table 1 for abbreviations and descriptions) were not selected for entry into the discriminant function equations. The percentage of total

Table 6

Means and Standard Deviations of 11 Structural Characteristics Measured at Nest-sites of Five Common Bird Species Nesting in Seven Farmstead Shelterbelts in Southern Minnesota in 1978 and 1979

Characteristic[b]	Common Grackle (N = 335)	Mourning Dove (N = 136)	American Robin (N = 87)	Gray Catbird (N = 17)	Chipping Sparrow (N = 14)
HTNT*	6.27 ± 3.51^{drcs}	2.26 ± 1.40^{g}	2.46 ± 1.88^{g}	1.26 ± 0.64^{g}	1.08 ± 0.66^{g}
DICA*	2.43 ± 1.79^{drc}	3.15 ± 1.14^{g}	2.93 ± 1.57^{g}	3.01 ± 1.18^{g}	2.74 ± 1.33
DINT*	0.23 ± 0.62^{ds}	0.51 ± 0.62^{grc}	0.27 ± 0.50^{dcs}	0.12 ± 0.30^{drs}	0.63 ± 0.66^{grc}
HTGC*	0.30 ± 0.32^{drcs}	0.39 ± 0.35^{gcs}	0.39 ± 0.35^{gcs}	1.05 ± 0.78^{gdrs}	0.60 ± 0.54^{gdrc}
PTGC*	44.8 ± 38.3^{rcs}	47.6 ± 36.2^{rcs}	64.3 ± 37.9^{gd}	77.9 ± 32.2^{gd}	79.3 ± 30.8^{gd}
STLE*	0.36 ± 1.98^{cs}	0.65 ± 2.09^{cs}	0.31 ± 1.41^{cs}	9.88 ± 5.55^{gdrs}	2.79 ± 4.97^{gdrc}
STMO*	0.14 ± 0.74^{c}	0.15 ± 0.58^{c}	0.16 ± 0.57^{c}	0.53 ± 0.62^{gdrs}	0.07 ± 0.27^{c}
CLOS*	39.3 ± 27.8^{drcs}	56.6 ± 26.2^{grcs}	63.7 ± 25.1^{gdcs}	96.5 ± 4.9^{gdr}	94.2 ± 5.4^{gdr}
HTTR*^{n}	10.07 ± 5.48^{drcs}	7.16 ± 3.81^{gcs}	6.92 ± 4.29^{gc}	3.34 ± 1.84^{gdr}	4.26 ± 2.87^{gd}
DITR*^{n}	0.08 ± 0.06^{drcs}	0.05 ± 0.05^{gr}	0.06 ± 0.04^{gdcs}	0.03 ± 0.03^{gr}	0.02 ± 0.02^{gr}
COMP^{n}	218.7 ± 100.8	228.6 ± 88.2	225.9 ± 76.5	233.1 ± 84.6	225.0 ± 58.5

[a] N = 589.

[b] Characteristics are listed in order of decreasing importance in discriminating among bird species in stepwise discriminant function. Characteristics indicated by an asterisk are significantly different among species ($P < 0.05$, single-classification ANOVA, Sokal and Rohlf [1969]); superscript n indicates not included in the discriminant function equations (see text). Superscripts, g, d, r, c and s indicate that a mean for a particular characteristic is different ($P < 0.05$, Student-Newman-Keuls test) from mean of Common Grackle, Mourning Dove, American Robin, Gray Catbird, or Chipping Sparrow, respectively. Descriptions and abbreviations of characteristics are from Table 1.

nest-sites accurately classified to bird species averaged 51.1% and ranged from 0.0% in sparrows to 88.1% in grackles (Table 7).

Stepwise discriminant analysis extracted four canonical variables (CV) or linear combinations of the 11 structural characteristics measured at

Table 7

Jackknifed Classification Matrix Giving the Percentage of Nests Correctly Classified to Bird Species and the Numbers of Nests Categorized into Each of the Five Common Bird Species Based on 11 Structural Characteristics Measured at 589 Nest-sites

Bird species	Percentage correct	Number of nests classified/bird species				
		Common Grackle	Mourning Dove	American Robin	Gray Catbird	Chipping Sparrow
Common Grackle	88.1	295	19	17	4	0
Mourning Dove	62.5	28	85	18	5	0
American Robin	34.5	22	33	30	2	0
Gray Catbird	70.6	2	1	2	12	0
Chipping Sparrow	0.0	0	4	7	3	0
Total	—	347	142	74	26	0

Table 8

Eigenvalues, Discriminating Information, Group (Bird Species) Canonical Correlation Coefficients and Standardized Coefficients of Eight Structural Characteristics for Canonical Variables 1 and 2 Extracted from Stepwise Discriminant Analysis of Between-species and Within-species Covariance Matrices of 11 Structural Characteristics Measured at Nest-sites (N = 589) of Five Common Bird Species

	Canonical variable[a]	
	1	2
Eigenvalue	1.038	0.474
Percentage of discriminating information	65.1	29.7
Bird species		
Common Grackle	−0.75	−0.30
Mourning Dove	0.71	0.67
American Robin	0.72	0.69
Gray Catbird	3.73	−2.90
Chipping Sparrow	2.17	−0.02
Structural characteristic[b]		
HTNT	−0.23	−0.25
DICA	0.24	0.12
DINT	0.16	0.29
HTGC	0.75	−0.09
PTGC	0.01	0.00
STLE	0.19	−0.40
STMO	−0.27	0.43
CLOS	0.01	0.00

[a] Canonial variables 1 and 2 are both significant ($P < 0.001$) based on Wilks' Λ criterion computed as a function of the eigenvalues using Bartlett's χ^2 approximation (Cooley and Lohnes 1971:249). Wilks' $\Lambda = 0.31$ and 0.63; $\chi^2 = 685$ and 272; df = 44 and 30, respectively.

[b] Descriptions and abbreviations of structural characteristics are from Table 1. Characteristics not included in discriminant equations (Table 6) are omitted.

nest-sites, which best segregated among the five common bird species. Only CV1 and CV2 afforded a significant ($P < 0.001$) degree of discrimination (Table 8). CV1 is a "herbaceous" variable because it principally includes the structural variable HTGC, although HTNT, DICA and STMO are important also, as indicated by relatively high standardized coefficients (after Raphael 1981, Williams 1981). CV1 accounts for 65.1% of the discriminating information that is available in the 11 characteristics measured at nest-sites to separate bird species. CV2 is termed a "woody stem" variable because it mainly associates the variables STLE and STMO. CV2 explains 29.7% of the discriminating information. CV3 and CV4 are neither biologically interpretable nor statistically significant ($P > 0.05$), and

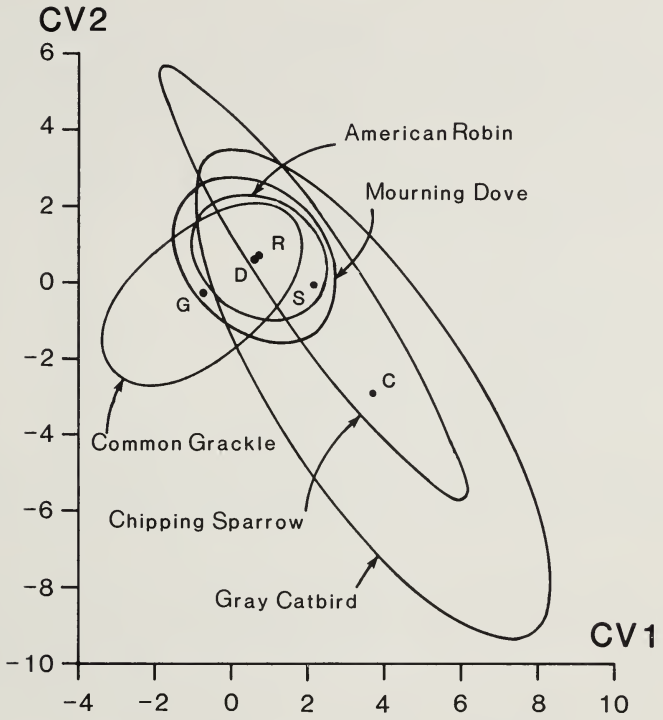


FIG. 1. Plot of group means of bird species for CV1 and CV2 (Table 8) and 95% confidence ellipses for the species' cases (nests) on CV1 and CV2 using the principal axes technique (Sokal and Rohlf 1969, Dueser and Shugart 1979). Group means: G = Common Grackle, D = Mourning Dove, R = American Robin, C = Gray Catbird and S = Chipping Sparrow.

account for only 3.7 and 1.5%, respectively, of the discriminating information.

A plot of the two principal canonical variables, CV1 on CV2 (Fig. 1), gives the best visual and ecologically interpretable illustration of the differences in the structural characteristics of nest-sites among the five common bird species. The relatively narrow, elongated ellipses of grackles, catbirds and sparrows (Fig. 1) indicate that most variance could be explained by CV1 (Table 8) (see Sokal and Rohlf 1969). In contrast, the more circular ellipses of robins and doves suggest that CV1 and CV2 were of nearly equal importance in discriminating nest-sites of these species. Species with group means to the right in Fig. 1 along the "herbaceous" variable, such as the catbird and the sparrow, were characterized by well-hidden nests. Nests of these two species were located close to the ground

TABLE 9

STRUCTURAL NESTING OVERLAP, NO_{ST}, BETWEEN PAIRS OF FIVE COMMON BIRD SPECIES NESTING IN SEVEN FARMSTEAD SHELTERBELTS IN SOUTHERN MINNESOTA IN 1978 AND 1979

Bird species pair	NO_{st} (%)[a]
Common Grackle—Mourning Dove	33
Common Grackle—American Robin	33
Common Grackle—Gray Catbird	9
Common Grackle—Chipping Sparrow	8
Mourning Dove—American Robin	69
Mourning Dove—Gray Catbird	20
Mourning Dove—Chipping Sparrow	26
American Robin—Gray Catbird	14
American Robin—Chipping Sparrow	20
Gray Catbird—Chipping Sparrow	34

[a] NO_{st} is calculated from 95% confidence ellipses for species' cases (nests) on canonical variables 1 and 2 (Fig. 1) by the ratio of the area of overlap for two species relative to the cumulative area for that pair of species (after Dueser and Shugart 1979).

and were well concealed by herbaceous vegetation (Table 6), compared to nests of other species. On the other hand, the mean of the grackle nests was located to the left in Fig. 1 because nests were often high above ground and well exposed. Means of dove and robin nests were intermediate in height above ground and percentage of herbaceous cover.

The position of group means along the "woody stem" variable essentially separates catbird nests from those of the other four species (Fig. 1), based on the density of woody stems surrounding nests (Table 6). Further, catbird and grackle nests tended to be located near the main stem of the nesting substrate relative to the location of nests of the other three species.

Structural nesting breadth, NB_{st}, or the relative variability in the distance of each species' nest from its respective group mean in 4-dimensional hyperspace (corresponding to four canonical variables) was greatest in grackles (NB_{st} = 1.97), followed by those of robins (1.89), sparrows (1.12), doves (1.08) and catbirds (0.89). As with NO_{su} (Table 5), structural nesting overlap, NO_{st}, in 2-dimensional hyperspace (Fig. 1) was greatest between doves and robins (69%, Table 9). NO_{st} of catbirds with sparrows and NO_{st} of grackles with either doves or robins were nearly equal (33–34%). The least amount of shared use of structural characteristics of nestsites was shown between grackles and either catbirds or sparrows (8–9%).

DISCUSSION

Suitability of shelterbelts as nesting habitat.—Farmstead shelterbelts are valuable habitats to avifauna in regions of intensive agriculture in

terms of both numbers of breeding species and density of nests (Table 2). The importance of these "wooded islands" is supported perhaps by comparisons to studies conducted in other types of habitats in the midwest region (e.g., see Skinner 1975, George et al. 1979). Studies of avifauna associated with farmstead shelterbelts report large numbers of nests for certain species, particularly grackle, dove and robin nests (see Randall 1955, LaPointe 1958, Field 1971, Martin 1978). In my study, 50.5, 20.5 and 13.1% of total nests (N = 617) were of these three species, respectively (Table 2).

A variety of factors may contribute to the suitability of farmstead shelterbelts as nesting habitat to different bird species in addition to the availability of preferred nesting substrate (Tables 3 and 4), and/or the microhabitat configuration afforded by the substrate (Tables 6 and 8, Fig. 1). One factor may include the spacing pattern used by landowners in planting trees and shrubs within and between rows of shelterbelts and its concomitant effect on vegetative structure. For example, the distance between permanent trees in rows after thinning may be as much as 5–7 m (see Smith and Scholten 1980). This planting practice probably creates favorable nesting areas for bird species adapted to mixed-breeding habitats, i.e., habitats with relatively open overstory canopies and/or dense cover near the ground for nest-sites (Table 6, Fig. 1) (after Gates and Gysel 1978, Stauffer and Best 1980).

The manner in which landowners maintain shelterbelts may also affect their importance to birds as nesting areas (see Read 1964, Smith and Scholten 1980 for maintenance procedures). For instance, younger shelterbelts (≤5 years) often are mowed to remove undesirable vegetation which compete for moisture with tree and shrub seedlings (George 1943). Mowing of dense undergrowth in a 5-year-old shelterbelt may have enabled an Eastern Meadowlark (*Sturnella magna*) to nest in 1978 (Table 2); meadowlark nests are typically characteristic of open, non-wooded habitats (George et al. 1979). Removal of snags is a practice that likely reduces the suitability of shelterbelts for primary and secondary cavity nesters (see Hardin and Evans 1977, Martin 1978, Stauffer and Best 1980). Although Black-capped Chickadees and Downy Woodpeckers were two cavity-nesting species observed in shelterbelts during spring (Yahner 1980a), neither nested in shelterbelts as a probable consequence of few snags and/or small size of shelterbelts. Two known cavities were present in the seven shelterbelts, and those were used as nest-sites by a House Sparrow (*Passer domesticus*) and a Starling (*Sturnus vulgaris*) in 1979 (Table 2).

The attractiveness of farmstead shelterbelts as nesting habitat to a particular bird species conceivably depends on many factors not considered in this study. Among these are type, quantity and availability of food (after

Franzreb 1978), including food items procured in shelterbelts or in contiguous habitats around farmsteads. For example, the probability of an American Robin selecting a shelterbelt as a nesting area may be contingent not only on the presence of *Picea* as nesting substrate (Table 4) but also on proximity of a preferred foraging area near the nest-site. Perhaps a mowed lawn, used as a foraging site and adjacent to the shelterbelt, contains sufficient food resources that were otherwise unavailable or in low abundance within the shelterbelt for raising a brood of robins. Another factor determining use of shelterbelts may be the ability of a bird species to tolerate disturbances associated with farm operations (after Emlen 1974, Cooke 1980). Shelterbelts are usually planted within 30–35 m of homes and buildings (Smith and Scholten 1980), and the disturbances created by humans, domestic animals and farm machinery may disrupt nesting activities of some species more than others. Two additional factors may be that some shelterbelts are narrower than the minimum width of a habitat required by certain breeding species (Stauffer and Best 1980), or that a less aggressive species benefits by the presence of a coexisting, more aggressive species (e.g., catbird) which effectively defends nesting areas against predation and parasitism (Clark and Robertson 1979). Finally, the presence of mammalian nest predators, such as red squirrels (*Tamiasciurus hudsonicus*), in certain types of shelterbelts (Nelson 1976, Yahner 1980b) may influence the overall suitability of these habitats as nesting areas.

Nest-site selection: substrate and structural considerations.—Farmstead shelterbelts represent an excellent habitat in which to examine patterns of nest-site selection for two reasons. First, the number of suitable nest-sites per bird species is presumably restricted by the limited number of trees and shrubs available (N = 3589 or 1089 plants/ha, this study). Second, nesting substrate among shelterbelts differed with regard to plant species (N = 31) as well as physiognomy.

The five common bird species preferred certain nesting substrate; use of specific woody species for nest-sites was not proportional to the actual number of individual plants per tree or shrub species in the seven shelterbelts (Table 4). These results agree with other studies dealing with doves and grackles (e.g., McClure 1946, LaPointe 1958, Field 1971). Moreover, grackle, dove and robin nests were each found in 16 different woody species (Table 1), but the relative proportions of total nests per woody species were less variable in grackles compared to doves and robins. As a consequence, NB_{su} was highest in the grackle (Table 4). Using NB_{su} as an inverse index of specialization (Levins 1968, Dueser and Shugart 1979) in use of substrate, the grackle may be classified as a generalist or opportunist along a generalist-specialist continuum. At the opposite pole of

the NB_{su} continuum are specialists (low NB_{su}), the catbird and the sparrow. The dove and the robin are positioned toward the middle of the continuum with intermediate values of NB_{su}.

Variability in location of nest-sites, based on structural characteristics (Table 6) and expressed by values of NB_{st}, may be viewed as a generalist-specialist continuum in discriminant 4-space (corresponding to canonical variable 1–4). Again, the grackle, followed by the robin, was less stereotyped in nest-site selection compared to the other three common species. Thus, both measures of nesting breadth were broad in the grackle and the robin but varied from intermediate to narrow with the other species, depending on the measure of breadth. For example, the sparrow was very specific in its choice of nesting substrate ($NB_{su} = 0.08$, Table 4) but was more flexible in selecting the location of nests relative to structural features ($NB_{st} = 1.12$) when compared to the dove or the catbird. Conversely, the dove was capable of using many woody plants ($NB_{su} = 0.31$) yet was stereotypic in terms of structural nesting breadth ($NB_{st} = 1.08$). In short, NB_{su} was not necessarily related to NB_{st} in comparisons within or among common bird species.

Because of the spatially-limited environment of shelterbelts, a certain amount of overlap in both use of specific nesting substrate and structural characteristics surrounding nest-sites is plausible among bird species (after Raphael 1981). NO_{su} and NO_{st} was greatest between doves and robins (Tables 5 and 9), partially the result of the use of robin nests by doves (e.g., McClure 1946, Weeks 1980, pers. obs.). Further, nests of these two species were often indistinguishable (Table 7) on the basis of high NO_{st} (Table 9) and similar mean values for 8 of the 11 structural characteristics (Table 6). On the other extreme, ecological requirements of some species in choice of nest-sites were so different (Tables 4 and 6) that little overlap in substrate use of structural characteristics was expected. For example, NO_{su} and NO_{st} were only 11 and 9%, respectively, between grackles and catbirds (Tables 5 and 9). Only 4 (1.2%) of 335 grackle nests were inaccurately classified as catbird nests (Table 7). Although the group mean of sparrows was segregated from means of each of the other species ($P < 0.001$), all nests ($N = 14$) were classified as being those of dove, robin or catbird (Table 7). This may be partially due to moderate amounts of cumulative overlap by sparrows with these three species in selection of microhabitat for total nest-sites (Table 6 and 9). Alternatively, a structural characteristic(s) not considered in this study may have given better discrimination between nest-sites of sparrows and those of the other three species, perhaps giving better accuracy in classification (see Raphael 1981 for additional discussion). Perhaps sample size was a factor in classification, yet 70.6% of catbird nests ($N = 17$) were categorized accurately (Ta-

ble 7). Yahner (in press) has shown that abundance of this sparrow in both spring and summer is correlated ($P < 0.05$) to the extent of the perimeter of shelterbelts; thus, "edge" of shelterbelts or nesting substrate (NB_{su} = 0.08, Table 4) may be relatively more important than structural features (Table 6) in choice of nest-sites by this species. In short, these small "wooded islands" were sufficiently heterogeneous to allow the five common bird species to select distinct nest-sites (Table 8, Fig. 1), thereby permitting high densities of nests compared to non-wooded habitats in the midwest. If more data were available to quantify patterns of nest-site selection by the 12 other species known to nest in these seven shelterbelts (Table 2), comparisons could be made to test whether or not the five common species were more abundant because of more generalized ecological requirements for nests.

Patterns of nest-site selection: management implications.—A knowledge of patterns of nest-site selection by bird species in shelterbelts may be helpful in formulating effective decisions pertaining to the future design of these farmstead habitats. For instance, based on NB_{su} (Table 4) and NB_{st} the grackle is extremely opportunistic in selection of nest-sites. This species appears capable of exploiting a variety of tree and shrub species (Table 4), with perhaps the only requirement being that the shelterbelt have some tall trees for nest-sites well-above ground level (Table 6, Fig. 1). Because nesting overlap between doves and robins was relatively extensive (Tables 5 and 9), management decisions for the design and the maintenance of shelterbelts may have similar effects on these two species. Stauffer and Best (1980), for example, concluded that partial removal of woody canopy in closed-canopy riparian woodlands would benefit both doves and robins. Thus, the partially-opened canopy that often occurs in farmstead shelterbelts due to spacing and thinning of trees and shrubs likely has similar effects on both of these species. But when spruce (*Picea* spp.), the preferred nesting substrate for doves and robins (Table 4), are planted close together (e.g., 3–4 m), the lower branches typically lose needles if contact is made with contiguous trees or shrubs due to shading (Smith and Scholten 1980). Doves and robins rarely constructed nests in lower (<3 m above ground), defoliated branches of spruce, perhaps because nest-sites of both species required a moderate amount of concealment (Table 6, Fig. 1). Loss of needles in lower branches also can reduce the effectiveness of spruce as wind barriers. Thus, an approximate spacing of 5–6 m between adjacent trees may help retain foliage, thereby serving a dual function of providing a long-term wind barrier and a nesting substrate for two common bird species in shelterbelts (H. Scholten, pers. comm.).

Catbirds, and to some extent sparrows, exhibited relatively narrow nest-

ing breadths and reduced overlap with those of other species (Tables 4, 5 and 9; Fig. 1). Because of stereotypic nest-site selection, an obvious management recommendation is to provide preferred nesting substrate (Table 4). Moreover, nests of these two species (particularly catbirds) were well concealed but close to ground level (Table 6, Fig. 1). Therefore, removal of herbaceous or woody vegetation (i.e., via mowing) should be restricted to areas between rows and attempts should be made to retain vegetation within a 0.5-m radius of branches of preferred shrubs (e.g., tartarian honeysuckle) or trees (e.g., Colorado blue spruce) (Table 4).

SUMMARY

Avian nest densities and nest-site selection were examined in seven Minnesota farmstead shelterbelts for two years. A total of 617 nests belonging to 17 bird species was noted. Suitability of shelterbelts as nesting habitats was determined by nest densities which were greater than those reported for non-wooded habitats in the region. Choice of nesting substrate by the total avian community or by individual bird species was not random. Nests-sites were segregated among the five most common bird species based primarily on two linear combinations of 11 structural characteristics termed as "herbaceous" or "woody stem" variables. The five common bird species were positioned along a generalist-specialist continuum in selection of nest-sites using two measures of nesting breadth. Measures of nesting overlap varied considerably between pairs of species.

Farmstead shelterbelts, despite their small size, are important nesting habitats for birds. These "wooded islands" are sufficiently heterogenous to permit the coexistence of several nesting species at high densities. Information about nest-site choice should be used by designers of shelterbelts for the benefit of certain breeding birds in the midwest.

ACKNOWLEDGMENTS

I am grateful to H. Scholten of the College of Forestry, University of Minnesota, and C. Wilcox of the Rosemount Agricultural Experiment Station for their cooperation with all aspects of the study. I also thank M. Weller and J. Cooper of the Department of Entomology, Fisheries and Wildlife, University of Minnesota, and H. Scholten for comments on an earlier draft of the manuscript. Several helpful comments were given also by J. C. Barlow, R. F. Johnston and J. D. Rising. This study was supported by the Minnesota Agricultural Experiment Station, and by grants from the Graduate School of the University of Minnesota, the National Rifle Association of America and the Max McGraw Wildlife Foundation. This paper is No. 11,196 of the Minnesota Agricultural Experiment Station, Scientific Journal Series, University of Minnesota, St. Paul.

LITERATURE CITED

Cassel, J. F., W. E. Moore, L. Strand, H. Voigt, R. Kroodsma and J. Larry. 1966. Breeding birds of some shelterbelts in Barnes County, North Dakota. Audubon Field Notes 20:649–655.

———, W. Buresh, J. Cassel, D. Fortney and G. Moen. 1967. Breeding birds of some North Dakota shelterbelts—III. Audubon Field Notes 21:650–656.

Clark, K. L. and R. J. Robertson. 1979. Spatial and temporal multi-species aggregations in birds as anti-parasite and anti-predator defenses. Behav. Ecol. Sociobiol. 5:359–371.

COOKE, A. S. 1980. Observations on how close certain passerine species will tolerate an approaching human in rural and suburban areas. Biol. Conserv. 18:85–88.

COOLEY, W. W. AND P. R. LOHNES. 1971. Multivariate data analysis. John Wiley and Sons, New York, New York.

DIXON, W. J. AND M. B. BROWN. 1979. Biomedical computer programs P-series. Univ. California Press, Berkeley, California.

DUESER, R. D. 1979. Niche pattern in a forest-floor small mammal fauna. Ecology 60:108–118.

——— AND H. H. SHUGART, JR. 1978. Microhabitats in a forest-floor small mammal fauna. Ecology 59:89–98.

EMLEN, J. T. 1974. An urban bird community in Tucson, Arizona: derivation, structure, regulation. Condor 76:184–197.

EMMERICH, J. M. 1978. Bird utilization of woodland habitat in the eastern quarter of South Dakota. M.S. thesis. South Dakota State Univ., Brookings, South Dakota.

FIELD, N. H. 1971. Use of an eastern South Dakota shelterbelt by nesting birds. South Dakota Bird Notes 23:43–45.

FRANZREB, K. E. 1978. Tree species used by birds in logged and unlogged mixed-coniferous forests. Wilson Bull. 90:221–238.

GATES, J. E. AND L. W. GYSEL. 1978. Avian nest dispersion and fledging success in field-forest ecotones. Ecology 59:871–883.

GEORGE, E. J. 1943. Effects of cultivation and number of rows on survival and growth of trees in farm windbreaks on the northern Great Plains. J. Forest. 41:820–828.

GEORGE, R. R., A. L. FARRIS, C. C. SCHWARTZ, D. D. HUMBURG AND J. C. COFFEY. 1979. Native prairie grass pastures as nest cover for upland birds. Wildl. Soc. Bull. 7:4–9.

GREEN, R. H. 1979. Sampling design and statistical methods for environmental biologists. John Wiley, New York, New York.

GRIFFITH, P. 1976. Introduction of the problems. Pp. 3–7 *in* Shelterbelts on the Great Plains (R. W. Tinus, ed.). Great Plains Agric. Council Publ. 78.

HARDIN, K. I. AND K. E. EVANS. 1977. Cavity nesting bird habitat in the oak-hickory forests . . . a review. USDA For. Serv. Tech. Rept. NC–30.

HARRISON, H. H. 1975. A field guide to birds' nests. Houghton Mifflin Co., Boston, Massachusetts.

JOHNSON, D. H. 1981. The use and misuse of statistics in wildlife habitat studies. Pp. 11–19 *in* The use of multivariate statistics in studies of wildlife habitats (D. E. Capen, ed.). USDA For. Serv. Gen. Tech. Rept. RM–87.

LACHENBRUCH, P. A. 1975. Discriminant analysis. Hafner Press, New York, New York.

LAPOINTE, D. F. 1958. Mourning Dove production in a central Nebraska shelterbelt. J. Wildl. Manage. 22:439–440.

LEVINS, R. 1968. Evolution in changing environments. Princeton Univ. Press, Princeton, New Jersey.

LOKEMOEN, J. T. AND H. F. DUEBBERT. 1976. Ferruginous Hawk nesting ecology and raptor populations in northern South Dakota. Condor 78:464–470.

MARTIN, T. E. 1978. Diversity and density of shelterbelt bird communities. M.S. thesis. South Dakota State Univ., Brookings, South Dakota.

MCCLURE, H. E. 1946. Mourning Doves in Nebraska and the west. Auk 63:24–42.

MILLER, H. W. AND D. H. JOHNSON. 1978. Interpreting the results of nesting studies. J. Wildl. Manage. 42:471–476.

NELSON, G. 1976. Mourning Dove nesting success in artificial and natural nests in central Minnesota. Proc. Iowa Acad. Sci. 83:112–115.

OLSON, R. A. AND L. D. FLAKE. 1975. Nesting of Ring-necked Pheasants in eastern South Dakota. Proc. South Dakota Acad. Sci. 54:126–136.

Orendurff, C. F. 1941. The first wildlife inventory of Nebraska shelterbelts. Nebraska Bird Rev. 9:7–8.

Parker, J. W. 1972. A mirror and pole device for examining high nests. Bird-Banding 43:216–218.

Petraitis, P. S. 1979. Likelihood measures of niche breadth and overlap. Ecology 60:703–710.

Pianka, E. R. 1973. The structure of lizard communities. Ann. Rev. Ecol. Syst. 4:53–74.

Randall, R. N. 1955. Mourning Dove production in south central North Dakota. J. Wildl. Manage. 19:157–159.

Raphael, M. G. 1981. Interspecific differences in nesting habitat of sympatric woodpeckers and nuthatches. Pp. 142–151 *in* The use of multivariate statistics in studies of wildlife habitat (D. E. Capen, ed.). USDA For. Serv. Gen. Tech. Rept. RM–87.

Read, R. A. 1964. Tree windbreaks for the central Great Plains. USDA For. Serv. Agric. Handbook No. 250.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185: 27–39.

Skinner, R. M. 1975. Grassland use patterns and prairie bird populations in Missouri. Pp. 171–180 *in* Prairie: a multiple view (M. K. Wali, ed.). North Dakota Press, Grand Forks, North Dakota.

Smith, M. and H. Scholten. 1980. Planting trees for farmstead shelter. Univ. Minnesota Agric. Ext. Serv. Bull. 196.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco, California.

Stauffer, D. G. and L. B. Best. 1980. Habitat selection by birds of riparian communities: evaluating effects of habitat alterations. J. Wildl. Manage. 44:1–15.

Weeks, H. P., Jr. 1980. Unusual egg deposition in Mourning Doves. Wilson Bull. 92:258–260.

Weiser, C. and D. J. Hlavinka. 1956. Comparisons of breeding-bird populations of three deciduous shelterbelts. Audubon Field Notes 10:416–419.

Williams, B. K. 1981. Discriminant analysis in wildlife research: theory and applications. Pp. 59–71 *in* The use of multivariate statistics in studies of wildlife habitats (D. E. Capen, ed.). USDA For. Serv. Gen. Tech. Rept. RM–87.

Yahner, R. H. 1980a. Breeding-bird censuses 111–117. Am. Birds 34:71–73.

———. 1980b. Burrow system use by red squirrels. Am. Midland Nat. 103:409–411.

———. In press. Seasonal dynamics, habitat relationships, and management of avifauna in farmstead shelterbelts. J. Wildl. Manage.

Yeaton, R. I. 1974. An ecological analysis of chaparral and pine forest bird communities on Santa Cruz Island and mainland California. Ecology 55:959–973.

DEPT. ENTOMOLOGY, FISHERIES, AND WILDLIFE, UNIV. MINNESOTA, ST. PAUL, MINNESOTA 55108. (PRESENT ADDRESS: FOREST RESOURCES LAB., SCHOOL OF FOREST RESOURCES, PENNSYLVANIA STATE UNIV., UNIVERSITY PARK, PENNSYLVANIA 16802). ACCEPTED 6 OCT. 1981.

Wilson Bull., 94(2), 1982, pp. 176–184

THE INFLUENCE OF SEASONALITY AND SELECTED WEATHER VARIABLES ON AUTUMN MIGRATION OF THREE SPECIES OF HAWKS THROUGH THE CENTRAL APPALACHIANS

KIMBERLY TITUS AND JAMES A. MOSHER

Few studies have reported the magnitude of autumn hawk migration through the central Appalachians. DeGarmo (1953) conducted a 5-year study of autumn hawk migration through West Virginia, but his data included full-season coverage from only a single point. Robbins (1950) reported hawk-count results obtained on a single day from 13 major and minor ridges in Maryland.

The physiographic features and weather associated with the large concentrations of migrating hawks in the northern-middle Atlantic states are well documented (see review in Haugh 1972, Brett and Nagy 1973, Dunne and Clark 1977). Unique physiographic features are absent from the ridge and valley system of the central Appalachians, as are the large concentrations of hawks such as those seen at Hawk Mountain (Brett and Nagy 1973) and at coastline sites (Allen and Peterson 1936, Mueller and Berger 1961, Hofslund 1966, Haugh 1972, Alerstam 1978).

Our objectives were to evaluate the influence of seasonality and selected weather variables on autumn hawk migration at two look-outs in the central Appalachians. Univariate and multivariate procedures were employed (see Richardson 1978) to evaluate the data which were collected according to the format recommended by the Hawk Migration Association of North America.

METHODS

Watches were conducted at Dan's Rock (39°35′N, 78°53′W) (Dan's Mountain) 1975–1979, located on the eastern edge of the Allegheny Front in western Maryland, Allegany County, at 822 m elev., and at High Rock (39°32′N, 79°6′W), Garrett Co., on Big Savage Mountain, 1977–1979, at 912 m elev. High Rock is 19 km west of Dan's Rock. Both lookouts provide excellent visibility in all directions and it is unlikely that the same hawks were counted at both look-outs since all observations were of hawks moving southwest, parallel to the ridges. Fig. 1 shows the orientation of the ridge system for the region and the location of the two look-outs.

Data were recorded on the standard forms of the Hawk Migration Association of North America. Weather data were obtained at the beginning of each hour and included temperature, maximum horizontal visibility, wind speed, wind direction and percent cloud cover. Neither site was monitored for the entire period of migration. At Dan's Rock, most weekends from 1 September–14 November were monitored; in 1977 and 1978, weekday periods were also monitored. At High Rock and at Dan's Rock in 1979, 4-h time periods were chosen

randomly for observation. We feel that a representative sample of all types of weather and migration volumes are proportionally correct with this protocol.

All statistical analyses were conducted using the Statistical Package for the Social Sciences (Nie et al. 1975). To reduce the degree of skewness, the hourly counts of the three dependent variables (number of Broad-winged Hawks [*Buteo platypterus*], Red-tailed Hawks [*B. jamaicensis*] and Sharp-shinned Hawks [*Accipiter striatus*]) were transformed using the natural logarithm + 1 (Richardson 1974, Alerstam 1978). The visibility variable was transformed with a square root function (Richardson 1974). No other independent variables were transformed; all had skewness and kurtosis values <1.5.

For analysis of weather variables, dates were chosen to encompass 95% of the typical migration period based on 5 years of observation (cf. Haugh 1972, Alerstam 1978). They were as follows: Broad-winged Hawk—1 September–4 October; Red-tailed Hawk—20 September–14 November; and for the Sharp-shinned Hawk—1 September–30 October.

Wilcoxon matched-pairs tests were conducted on five weather variables for which 57 h of simultaneous data existed at both ridges. The mean number of hawks migrating by each look-out was evaluated with Mann-Whitney *U*-tests to examine relative migration intensity at the two look-outs. A fixed effects, 2-way analysis of variance (ANOVA) was conducted to determine the possible interaction of wind speed and wind direction. Four wind speed categories (0–8, 9.6–16, 17.6–24, >25.6 km/h) were used. Wind direction was classified as either following or opposing (Richardson 1978). As the direction of migration was southwest, paralleling the ridges, winds from the south, southwest and west were considered as opposing winds, all other directions and calm–variable being considered following.

Examination of standardized error residuals from multiple regression showed strong autocorrelations in the data. The problem of error terms being serially correlated and failure to meet the appropriate levels of the Durbin-Watson test precluded the use of multiple regression techniques (Neter and Wasserman 1974, Richardson 1974). The data were analyzed using stepwise discriminant function analyses by reducing the dependent variable to a migration ($\geq$1 hawk/h) vs no migration analysis. Other recent migration studies that have used discriminant analysis in a similar manner include Able (1973), Richardson (1974), Alterstam (1978) and Beason (1978). As used in this study, discriminant analysis has both a predictive and an explanatory function. An explanation of the association of the independent variables with migration is achieved by examining the sign of the correlation of the canonical discriminant functions with the observation variables (cf. Able 1973, Williams 1981). The predictive or classification portion of discriminant analysis allows examination of the strength of the linear discriminant functions in achieving group separation. The stepwise selection criteria used minimized Wilk's lambda and thereby maximized the between groups F-ratio. For the discriminant analyses wind direction was coded with tail winds at 0° scaling to perpendicular winds at 90° and opposing winds at 180°.

RESULTS

Table 1 includes the total number of hawks observed at Dan's Rock and High Rock and species percentages compared with those for Hawk Mountain, Berks and Schuykill counties, Pennsylvania. At all locations the Sharp-shinned, Red-tailed and Broad-winged hawks make up over 75% of the total counts. The seasonal cycle of fall migration for these three species is given in Fig. 2 for both look-outs pooled. The peak flights of Sharp-shinned Hawks were from 5–15 October, and for Red-tailed Hawks from 20–30 October. The Broad-winged Hawk attained peak flights between

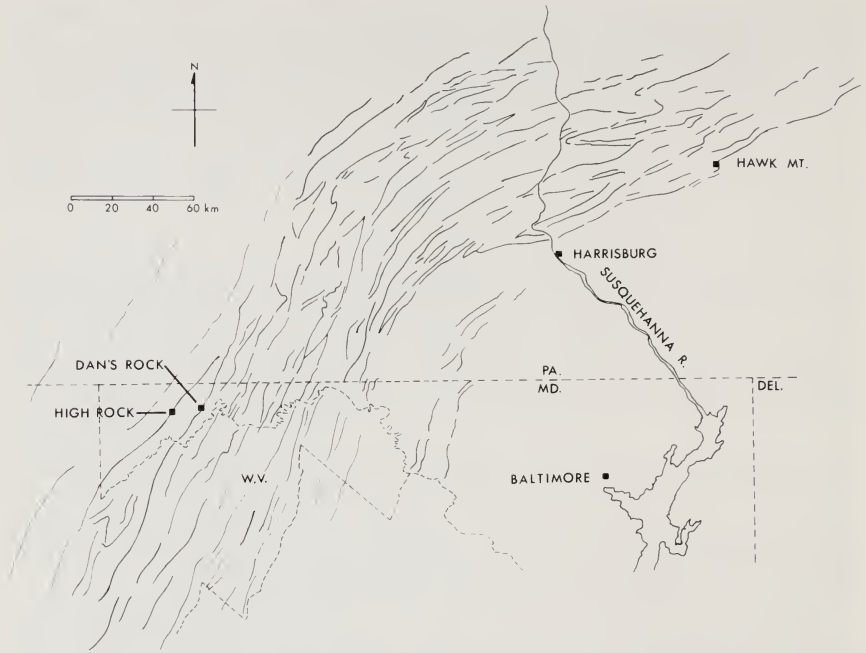


FIG. 1. The ridge system from eastern Pennsylvania southwest through West Virginia, including the two study sites in western Maryland.

15–25 September when 47% of the total flight occurred but a large drop-off in daily counts did not occur until after 30 September.

Results of the Mann-Whitney *U*-tests showed that the total number of hawks ($P < 0.001$), number of Red-tailed Hawks ($P < 0.01$), and number of Broad-winged Hawks ($P < 0.01$) were greater at Dan's Rock. No difference was found for the number of Sharp-shinned Hawks ($P > 0.05$). Comparing simultaneous weather data at the two look-outs revealed significant differences in visibility and temperature (both Wilcoxon matched-pairs test [$P < 0.01$]). Because of these differences, subsequent analyses treat each look-out separately.

The results of the 2-way ANOVA showed no interaction among the two wind directions and the four wind speed categories at High Rock for any of the three species ($P > 0.1$ in all cases). For the Broad-winged Hawk at High Rock winds >25 km/h had higher hourly counts based on Duncan's multiple range test (DMRT) (df = 3152, $P < 0.05$). Sharp-shinned Hawk flights at High Rock were greater when wind speeds were >9 km/h (DMRT) (df = 3197, $P < 0.05$). At Dan's Rock the only significant results

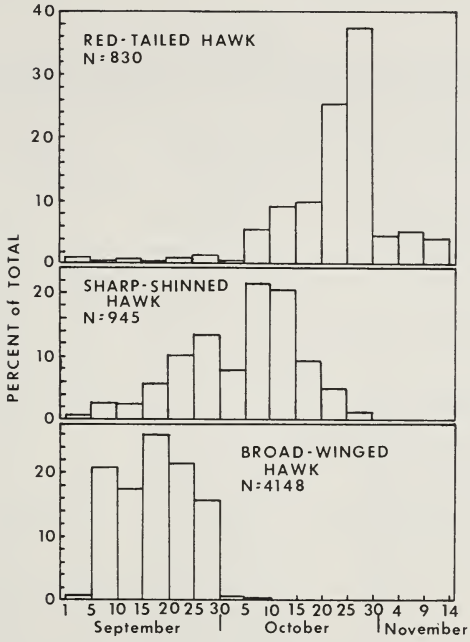


FIG. 2. Temporal distribution for three migrating hawk species at Dan's Rock and High Rock, Maryland, during the autumns of 1975–1979.

(df = 2462, $P < 0.01$) of the 2-way ANOVA were an interaction of wind speed and direction for the Broad-winged Hawk. Following winds >9 km/h had a higher number of Broad-winged Hawks/h (DMRT) ($P < 0.05$).

Three discriminant analyses were conducted on the Dan's Rock data (Table 2). For the Sharp-shinned Hawk the canonical correlation coefficient is low, even though the between groups F-statistic is significant. Migration tended to occur with following winds, good visibility and during later periods of the available migratory period. Classification was 26% above chance (Wiedemann and Fenster 1978) at Dan's Rock, and when the Dan's Rock discriminant function equation was used to predict migration at High Rock similar predictability was obtained. For the Broad-winged Hawk with a 35-day migratory period, migration tended to occur with strong following winds, good visibility, warm temperatures and during afternoon periods. Classification results were similar to those of the Sharp-shinned Hawk. The discriminant analysis of the Red-tailed Hawk data had a much higher canonical correlation and much better classification than for the other two species. The results revealed that migration tended to

TABLE 1

SUMMARY OF WESTERN MARYLAND FALL HAWK COUNTS AND SPECIES PERCENTAGES, INCLUDING HAWK MT., PENNSYLVANIA, 1975–1979

	Dan's Rock		High Rock		% of total	% of total for Hawk Mt.[a]
	1975–1979	%	1977–1979	%		
Accipiter gentilis (Goshawk)	4	0.07	0	0.00	0.05	0.33
A. striatus	641	10.90	311	20.59	12.89	15.45
A. cooperii (Cooper's Hawk)	86	1.46	25	1.66	1.50	0.75
Buteo jamaicensis	953	16.22	134	8.87	14.71	16.45
B. lineatus (Red-shouldered Hawk)	61	1.04	7	0.46	0.92	1.95
B. platypterus	3447	59.17	718	47.55	56.39	57.47
B. lagopus (Rough-legged Hawk)	2	0.03	0	0.00	0.03	0.06
Aquila chrysaetos (Golden Eagle)	7	0.12	0	0.00	0.09	0.22
Haliaeetus leucocephalus (Bald Eagle)	5	0.09	1	0.07	0.08	0.28
Circus cyaneus (Northern Harrier)	79	1.34	24	1.59	1.39	1.32
Pandion haliaetus (Osprey)	33	0.56	11	0.73	0.60	1.98
Falco peregrinus (Peregrine Falcon)	3	0.05	2	0.13	0.07	0.14
F. columbarius (Merlin)	2	0.03	0	0.00	0.03	0.12
F. sparverius (American Kestrel)	56	0.95	90	5.96	1.98	2.09
Unidentified	497	8.46	187	12.38	9.26	1.08
Total	5876	100.49	1510	99.99	99.99	99.69
Days	124	—	60	—	—	—

[a] From Haugh (1972) for 1954–1968.

occur when winds were opposing and light, visibility was good, temperature was high, cloud cover was low, and during later periods of the available migratory period.

DISCUSSION

The similarity of the species composition in western Maryland with that at Hawk Mountain suggests that these two sites are sampling similar interior migrant populations of hawks (see Nagy 1977). As lakes Erie and Ontario effectively shunt Canadian birds westward during the autumn migration (Haugh 1972), western Maryland flights probably represent birds that have entered the ridge and valley system in Pennsylvania only from points north and east.

The peak flights of Sharp-shinned Hawks at our sites coincided with that of Hawk Mountain (see Haugh 1972). At both locations a noticeable drop-off in flights occurred after 15 October. Peak flights of Red-tailed Hawks also exhibited a temporal similarity. The Broad-winged Hawk exhibited a different pattern in western Maryland from that of Hawk Mountain. The peak at Hawk Mountain was from 10–19 September, when about

TABLE 2

RESULTS OF DISCRIMINANT ANALYSES FOR NO MIGRATION COMPARED WITH MIGRATION ACCORDING TO SELECTED VARIABLES AT DAN'S ROCK, MARYLAND, 1975–1979

	Sharp-shinned Hawk		Broad-winged Hawk		Red-tailed Hawk	
	Sign of correction with migration[a]	P[b]	Sign of correction with migration	P	Sign of correction with migration	P
Wind direction	−	***	−	***	+	***
Wind speed	—	NS	+	**	−	***
Visibility	+	***	+	***	+	***
Temperature	—	NS	+	***	+	***
% cloud cover	—	NS	—	NS	−	***
Julian day (day of year)	+	***	—	NS	+	***
Hour	—	NS	+	***	—	NS
F-statistic	6.8	***	5.1	***	30.9	***
Number of hours	309	—	240	—	250	—
Canonical correction coeff.	0.250	—	0.313	—	0.658	—
% correct classification	63%	—	62%	—	86%	—
Cohen's Kappa (Kw)[c]	26%	—	23%	—	70%	—
% correct classification for High Rock	63%	—	66%	—	69%	—
Cohen's Kappa (Kw)	29%	—	26%	—	25%	—

[a] The sign of the pooled-within groups correlated between the canonical discriminant function and the discrimination variables. All signs are standardized.

[b] Levels of significance are as follows: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

[c] A chance corrected classification statistic (see Wiedemann and Fenster 1978).

75% of the Broad-winged Hawks migrated by, while in western Maryland only 42% had migrated by then. Thus, while the flights of Broad-winged Hawks dropped off greatly after 20 September at Hawk Mountain (Haugh 1972), in western Maryland moderate flights continued until the end of September.

The leading lines (topographical features that induce migrating birds to follow them [Mueller and Berger 1967a]) of the central Appalachians are probably quite important for migrating hawks because the ridges are long and prominent. The eastern edge of the Allegheny Front (Dan's Mountain) seems to be a major leading line through this portion of the Appalachians. Although High Rock is at a slightly higher elevation than Dan's Rock, the vertical drop of the eastern edge of the Allegheny Front is much greater, perhaps providing greater lift and a stronger leading line for concentrating hawks (Richardson 1978). This is consistent with Mueller and Berger's (1967a) views on the effectiveness of a leading line. Sharp-shinned Hawks, which did not migrate in higher numbers at Dan's Rock, may not require the greater lift provided by the Allegheny Front. Less prominent ridges

have a correspondingly smaller hawk flight based on a few days when lower elevation ridges to the east were monitored concurrently with Dan's Rock. Robbins (1950) found similar results based on his sampling of western Maryland ridges.

Mueller and Berger (1967b) found that the largest flights of Sharp-shinned Hawks occurred on strong westerly winds. No interaction between wind speed and direction was found in this study for Sharp-shinned Hawks although at High Rock wind speeds >9 km/h had higher hourly counts. The discriminant analysis for this species provided little predictability. The highest loading was on Julian day, indicating that the day of the season alone was the best predicting variable. For the Broad-winged Hawk the discriminant analysis results also showed low predictability. The highest canonical correlation coefficient and the highest percent correct classification was for the Red-tailed Hawk. Unlike the westerly wind component which produced peak hawk counts in many studies (see review in Richardson 1978) opposing winds and a southeasterly flow with clear, calm weather resulted in peak Red-tailed Hawk counts.

Few multivariate studies are available on hawk migration for comparison. Alerstam (1978), using stepwise discriminant analysis, had canonical correlation coefficients ranging from 0.48–0.60 when attempting to predict autumn hawk migration intensity at Falsterbo, Sweden. With over 30 variables, Beason (1978) was able to classify autumn water bird migration versus no migration with 80% correct classification while with only three variables, classification was 69% and Julian day was the important discriminating variable.

The results of this study seem to show that weather variables measured according to standard format (Hawk Migration Association of North America) have a low, but significant, predictive ability. Seasonality (Julian day) is probably the major predicting variable in determining the magnitude of autumn hawk migration in the central Appalachians, and the hour of the day apparently also influences migration patterns. Discriminant analysis, with only two groups, clarifies these points in a more simplistic manner than would multiple regression (Richardson 1974, 1978). Future researchers analyzing standardized HMANA data should compensate for the seasonality of migration (Richardson 1978).

SUMMARY

We compared the possible effects of weather, seasonality and topography on autumn hawk migration at two look-outs in the central Appalachians. Dan's Rock, located on the more prominent Allegheny Front, had more Red-tailed (*Buteo jamaicensis*) and Broad-winged (*B. platypterus*) hawks per hour than High Rock. The species composition of the flights was similar to those at Hawk Mountain, Pennsylvania.

For Sharp-shinned Hawks (*Accipiter striatus*), migration was associated with good visibility and following winds. Broad-winged Hawk migration was associated with good visibility, strong favorable winds, high temperatures and afternoon periods. Red-tailed Hawk migration was associated with light, opposing winds, characterized by southeasterly flows.

ACKNOWLEDGMENTS

We are especially indebted to A. and P. Smith who were responsible for the consistency of data collection at Dan's Rock and who shared their data with us. The authors wish to thank the 1977 and 1978 avian population classes of Frostburg State College, members of the Allegany Bird Club and many volunteers who assisted with the watches. We appreciate the helpful suggestions on an earlier draft of this manuscript by W. J. Richardson and the thoughtful reviews by K. P. Able and K. L. Bildstein. Computer time was provided by the Computer Science Center of the University of Maryland. This is contribution number 1274-AEL of the Appalachian Environmental Laboratory and Technical Report number 006 of the Central Appalachian Raptor Ecology Program.

LITERATURE CITED

Able, K. P. 1973. The role of weather variables and flight direction in determining the magnitude of nocturnal bird migration. Ecology 54:1031–1041.

Alerstam, T. 1978. Analysis and theory of visible migration. Oikos 30:273–349.

Allen, R. P. and R. T. Peterson. 1936. The hawk migrations at Cape May Point, New Jersey. Auk 53:393–404.

Beason, R. C. 1978. The influence of weather and topography on water bird migration in the southwestern United States. Oecologia 32:153–169.

Brett, J. J. and A. C. Nagy. 1973. Feathers in the wind. The mountain and the migration. Hawk Mt. Sanctuary Assoc., Kempton, Pennsylvania.

DeGarmo, W. R. 1953. A five year study of hawk migration. Redstart 20:39–54.

Dunne, P. J. and W. S. Clark. 1977. Fall hawk movement at Cape May Point, New Jersey–1976. New Jersey Audubon 3(7&8):114–124.

Haugh, J. R. 1972. A study of hawk migration in eastern North America. Search 2(16):1–59.

Hofslund, P. B. 1966. Hawk migration over the western tip of Lake Superior. Wilson Bull. 78:79–87.

Mueller, H. C. and D. D. Berger. 1961. Weather and fall migration of hawks at Cedar Grove, Wisconsin. Wilson Bull. 73:171–192.

——— and ———. 1967a. Wind drift, leading lines and diurnal migration. Wilson Bull. 79:50–63.

——— and ———. 1967b. Fall migration of Sharp-shinned Hawks. Wilson Bull. 79:397–415.

Nagy, A. C. 1977. Population trend indices based on 40 years of autumn counts at Hawk Mountain Sanctuary in northeastern Pennsylvania. Pp. 243–252 *in* Proc. World Conf. Birds of Prey, Vienna, 1975 (R. D. Chancellor, ed.). Int. Council for Bird Preserv.

Neter, J. and W. Wasserman. 1974. Applied linear statistical models. Richard D. Irwin, Inc., Homewood, Illinois.

Nie, H. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner and D. H. Bent (eds.). 1975. Statistical package for the social sciences. McGraw Hill, Inc., New York, New York.

Richardson, W. J. 1974. Multivariate approaches to forecasting day-to-day variations in the amount of bird migration. Pp. 309–329 *in* Proc. Conf. Biol. Aspects of the Bird/

Aircraft Collision Problem (S. A. Gauthreaux, Jr., ed.). Clemson Univ., Clemson, South Carolina.

———. 1978. Timing and amount of bird migration in relation to weather: a review. Oikos 30:224–272.

Robbins, C. S. 1950. Hawks over Maryland, fall of 1949. Maryland Birdlife 6:2–11.

Wiedemann, C. F. and C. A. Fenster. 1978. The use of chance corrected percentage of agreement to interpret the results of a discriminant analysis. Educ. Phychol. Measure. 38:29–35.

Williams, B. K. 1981. Discriminant analysis in wildlife research: theory and applications. Pp. 59–71 *in* The use of multivariate statistics in studies of wildlife habitat (D. Capen, ed.). USDA For. Serv. Gen. Tech. Rept. RM–87.

APPALACHIAN ENVIRONMENTAL LABORATORY, CEES, UNIV. MARYLAND, GUNTER HALL, FROSTBURG, MARYLAND 21532. ACCEPTED 6 OCT. 1981.

Wilson Bull., 94(2), 1982, pp. 185–197

RADIONUCLIDES IN MOURNING DOVES NEAR A NUCLEAR FACILITY COMPLEX IN SOUTHEASTERN IDAHO

O. Doyle Markham and Douglas K. Halford

The Idaho National Engineering Laboratory (INEL) Site in southeastern Idaho contains the world's largest concentration of nuclear reactors; to date some 52 reactors have been constructed and 17 reactors are still operable. In addition, the INEL contains a nuclear fuel reprocessing plant, terrestrial areas for the disposal of solid radioactive waste and leaching ponds for the disposal of contaminated liquid wastes. With the exception of uranium mining and fuel fabrication, the INEL activities include all of the nuclear fuel cycle.

Mourning Doves (*Zenaida macroura*) are ubiquitous game birds in Idaho and are common on the INEL during the summer (Reynolds and Trost 1981). They forage, obtain grit and/or drink water at or near these facilities (Trost et al. 1976, Halford and Millard 1978, Arthur and Markham 1978).

The potential exists for Mourning Doves at these facilities to ingest radionuclides. Since birds are the most mobile of the animals occurring near nuclear facilities and since doves are a popular game species, it is possible that radioactively-contaminated birds could be ingested by, and thus, provide a radiation dose to man. Other predators, such as raptors, could also ingest radionuclides by consuming doves. The purpose of this study was (1) to determine the concentrations of radionuclides in Mourning Dove tissues near various types of nuclear facilities, (2) to determine the consequent radiation dose to doves, (3) to determine the consequence of the transfer of radionuclides through the food chain and (4) to relate these concentrations to potential radiation doses to man.

STUDY AREAS

All but the control study area were located on or adjacent to the INEL Site (Fig. 1) which is a 231,600-ha area, administered by the U.S. Department of Energy, in the upper Snake River Plain in Butte, Jefferson, Bonneville, Clark and Bingham counties, Idaho. Public access to the INEL is controlled, and hunting is not permitted. The primary mission of the INEL is to conduct research and development programs in nuclear energy, geothermal and advanced energy sources, environment, safety and national security applications. The INEL became a National Environmental Research Park in 1975.

The vegetation on the INEL Site consists primarily of sagebrush (*Artemisia* sp.)-grass types (Harniss and West 1973, McBride et al. 1978); the predominant shrub is big sagebrush (*Artemisia tridentata*). Other prominent shrubs are rabbitbrush (*Chrysothamnus viscidiflorus*), winter fat (*Eurotia lanata*), snakeweed (*Gutierrezia sarothrae*) and shadscale (*Atriplex confertifolia*). The most common grasses are bottle brush squirrel tail (*Sitanion hystrix*),

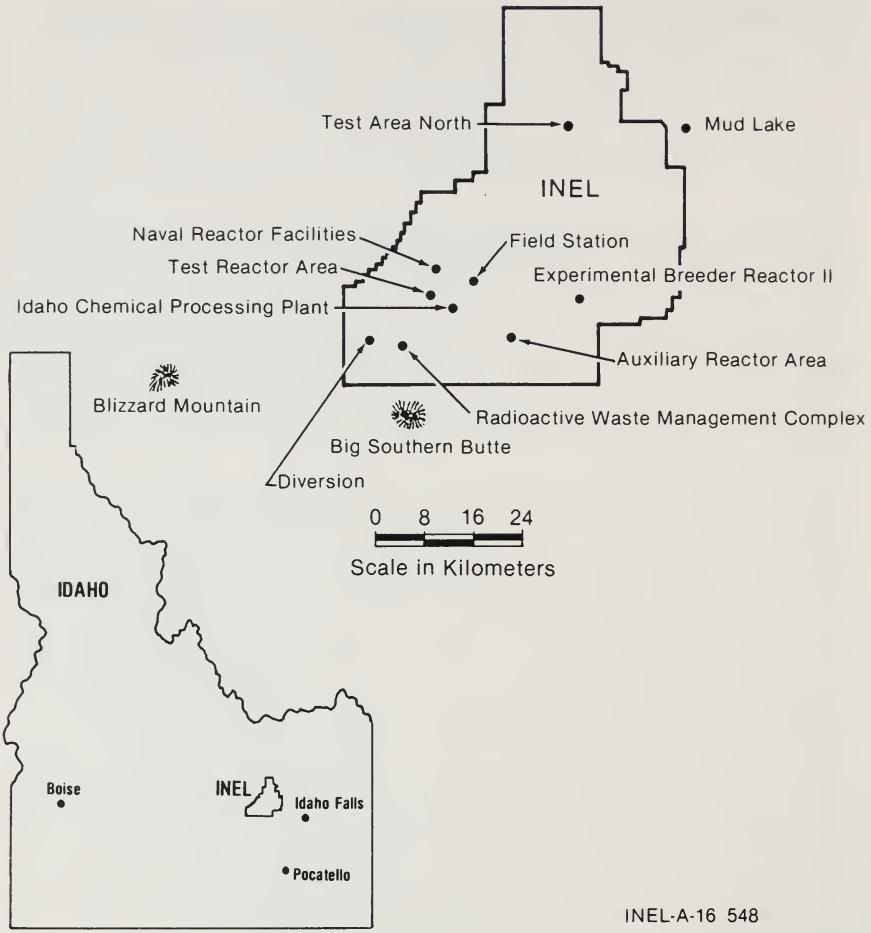


FIG. 1. Locations of Mourning Dove samples on and near the Idaho National Engineering Laboratory Site.

bluebunch wheatgrass (*Agropyron spicatum*), western wheatgrass (*A. smithii*), Indian ricegrass (*Oryzopsis hymenoides*), Great Basin wildrye (*Elymus cinereus*) and needle-and-thread grass (*Stipa comata*).

Doves were collected near seven nuclear facilities. One of these, the Test Reactor Area (TRA), is a nuclear materials testing complex which tests the performance of reactor materials and equipment components in high neutron flux. Since 1952 low-level liquid radioactive waste generated by three test reactors and their support facilities have been disposed of in radioactive leaching ponds adjacent to TRA. The ponds have an area of 1.5 ha. Approximately 48,000 curies (Ci) (1 Ci = 3.7×10^{10} nuclear transformations per second) of beta-gamma activation and fission radionuclides were released into the ponds by TRA facilities from 1952–1977 (White 1978). Radionuclides with half-lives (the time for the activity

to decrease by one-half) less than 1 year make up about 80% of this activity. Aquatic and littoral vegetation existing in this area have been previously described (Halford and Millard 1978).

The Radioactive Waste Management Complex presently contains two major waste disposal or storage facilities. The Subsurface Disposal Area (SDA) is a 36-ha area where low-level fission and activation waste from INEL facilities are disposed beneath the soil surface. In addition, plutonium and americium wastes were buried in the SDA prior to late 1970. After 1970, plutonium and americium wastes were stored above ground in the Transuranic Storage Area.

The Auxilary Reactor Area (ARA) contains a variety of development and research programs. Post-irradiation examination of materials and reactor components are carried out in this area. In addition, a reactor, the SL-1, was accidentally destroyed at this location in 1961 and contaminated the immediate surroundings.

Test Area North (TAN) contains several nuclear testing and support facilities. During this study the Loss-of-Fluids Test (LOFT) facility, which is currently investigating the capability of emergency core cooling systems when primary cooling systems failures and leaks are stimulated, was under construction.

The Naval Reactors Facility (NRF) contains four major installations. Three of these are nuclear prototype facilities for the testing and operation of nuclear reactors used to power various U.S. Navy vessels. Another facility receives, examines and prepares naval expended nuclear fuel for shipment to the Idaho Chemical Processing Plant. The Navy also conducts nuclear training for Navy personnel at these facilities. The primary water source of doves in the NRF area is probably two sewage leaching ponds.

The Idaho Chemical Processing Plant (ICPP) dissolves and recovers uranium from spent nuclear fuel and solidifies the resultant liquid waste. During these operations, trace amounts of radionuclides are released in the atmospheric effluents. The ICPP accounts for over 99% of the particulate radionuclides released into the atmosphere from INEL facilities (White 1978).

The Experimental Breeder Reactor-II (EBR-II) is a breeder reactor demonstration plant which also irradiates various reactor fuels and materials for the breeder reactor research program. In addition to EBR-II, three other test reactors, as well as various other nuclear facilities, exist at this location. Doves commonly drink water from either sewage leaching ponds or a waste water pond at this facility.

METHODS

From 29 May–26 July 1974, 252 Mourning Doves were collected periodically at seven on-site locations near nuclear facilities and at a control location (Blizzard Mt.) (Table 1, Fig. 1). From 23 June–14 August 1975, Mourning Doves were collected near the Test Reactor Area, the Idaho Chemical Processing Plant and the Radioactive Waste Management Complex, as well as at four locations on or near the INEL Site and a control area. In 1976 and 1977, additional samples were collected at TRA, ICPP and a control area.

Immediately following collection, the doves were taken to the laboratory. The entire gastrointestinal tract was removed and approximately 20–30 g of muscle tissue were dissected from the carcass. Each tissue sample was placed in a counting vial, weighed and frozen for later analyses. Samples were analyzed for gamma-emitting radionuclides with a 65 cm^3 germanium-lithium detector coupled to a computer-controlled multichannel analyzer.

During 1974 the estimated minimum detectable concentration (i.e., the minimum concentration in a sample that could be distinguished from instrumentation background determinations) for ^{137}Cs in Mourning Dove tissues was 0.4 pCi/g; the detection concentrations for

the other radionuclides were similar. However, during the remainder of the study, the minimum detectable concentration was 0.6 pCi/g. In calculating the mean concentrations, the value of the minimum detectable concentration was used for tissues which did not have detectable ^{137}Cs concentrations.

Since the data were not normally distributed, a nonparametric test, the Kruskal-Wallis test, was used to determine if differences in concentrations among locations or years existed at the <0.05 significance level, and a follow-up test, Dunn's Multiple Comparison Procedure, was used to identify which particular years or locations were significantly different. A significance level of $P < 0.15$ was used in the second test as recommended by Hollander and Wolfe (1973). Since dose determinations were based upon concentrations in tissues, statistical tests were not conducted on the dose data. Statistical relations between the radiation doses for the various years and locations would be similar to those for the radionuclide concentration data.

Potential whole-body dose commitment to man consuming contaminated Mourning Doves:

$$= \left(61 \frac{\text{mrem}}{\mu\text{Ci}} \cdot \frac{\text{X } \mu\text{Ci}_{^{137}\text{Cs in tissue}}}{\text{g}}\right) \cdot \left(\text{g of tissue consumed}\right)$$

where:

μCi = microcurie (1 μCi = 10^{-6} Ci)
X μCi/g = the number of microcuries per gram of tissue, and
mrem = 10^{-3} rem, rem is a unit in radiation protection which relates the absorbed dose to the risk of a resulting biological effect.

For calculations of dose commitment to humans, it was assumed that the Mourning Doves were killed and eaten immediately; biological elimination by the Mourning Doves and any reduction in radioactivity as a result of cooking were not considered in dose calculations; doses were based upon the assumption that a person ate only one Mourning Dove and the weight of the muscle consumed was 25% of the live weight.

Internal dose calculations for doves were made using muscle nuclide concentrations and assuming the radionuclides were in equilibrium with the body and uniformly distributed throughout the body. Using principles established by the I.C.R.P. (1968), the dose to doves from internally deposited radionuclides was calculated as follows:

$$H = 51.2EC \text{ rads}$$

where H = dose commitment (rad), rad is a unit of radiation dose; 51.2 (dis/MeV) (g-rad/d-μCi) is a constant
E = effective absorbed energy per disintegration (MeV/dis.; I.C.R.P. 1959); 0.37 (used value for spleen since this is the lowest E given for ^{137}Cs and doves are small birds so absorption would be minimal), and
C = radionuclide concentration in muscle (μCi/g),

therefore $H = 51.2\ (0.37)\ \frac{\text{X } \mu\text{Ci}}{\text{g}}$

RESULTS

Cesium-137 frequently occurred in Mourning Dove tissues from most of the study areas (Tables 1 and 2). Generally ^{137}Cs concentrations in tissues from the control area were near or below the detection limit. During all 4 years of the study, ^{137}Cs concentrations in muscle tissues of doves were

Table 1

Cesium-137 Concentrations (pCi/g) in Mourning Dove Muscle Tissue

Location	1974			1975			1976			1977		
	$\bar{x}$	Range	N	$\bar{x}$	Range	N	$\bar{x}$	Range	N	$\bar{x}$	Range	N
Test Reactor Area	1.57ab[1]	<0.4–6.9	17	4.05a	<0.6–24	16	1.48a	1.1–1.5	5	15.85a	<0.6–171	12
Idaho Chemical Processing Plant	3.24b	<0.4–11.6	16	0.84ab	<0.6–1.6	16	1.98a	0.7–5.3	4	—	—	—
Radioactive Waste Management Complex	0.58ac	<0.4–0.9	16	0.63ab	<0.6–0.8	12	—	—	—	—	—	—
Background (control)	0.44c	<0.4–0.8	16	0.75ab	<0.6–2.0	11	<0.6	<0.6	8	<0.6	<0.6	7
Test Area North	0.49ac	<0.4–1.1	16	—	—	—	—	—	—	—	—	—
Experimental Breeder Reactor II	0.40c	<0.4–0.6	16	—	—	—	—	—	—	—	—	—
Auxiliary Reactor Area	<0.40ac	<0.4	4	—	—	—	—	—	—	—	—	—
Naval Reactors Facility	<0.40ac	<0.4	4	—	—	—	—	—	—	—	—	—
Big Southern Butte	—	—	—	0.64b	<0.6–1.1	17	—	—	—	—	—	—
Diversion	—	—	—	<0.6b	<0.6	16	—	—	—	—	—	—
Field Station	—	—	—	0.62b	<0.6–0.8	12	—	—	—	—	—	—
Mud Lake	—	—	—	0.65ab	<0.6–1.0	11	—	—	—	—	—	—

[1] Concentration values in each column not followed by the same letter are significantly different (see text); e.g., during 1974, the TRA samples were significantly different from Background and Experimental Breeder Reactor II samples. The ICPP samples were significantly different from all of the other locations except the TRA.

Table 2

Cesium–137 Concentrations (pCi/g) in Mourning Dove Gastrointestinal Tracts

Location	1974			1975			1976			1977		
	$\bar{x}$	Range	N	$\bar{x}$	Range	N	$\bar{x}$	Range	N	$\bar{x}$	Range	N
Test Reactor Area	2.12ab[1]	<0.4–7.8	17	41.1a	<0.6–430	16	1.12a	<0.6–1.6	5	75.8a	<0.6–419	12
Idaho Chemical Processing Plant	14.75b	<0.6–139	16	2.3ab	<0.6–7.8	16	1.3a	<0.6–2.8	3	—	—	—
Radioactive Waste Management Complex	0.83a	<0.6–1.7	12	1.2abc	<0.6–4	12	—	—	—	—	—	—
Background (control)	1.08a	<0.6–7	16	1.6abc	<0.6–7	11	0.8a	<0.6–1.2	8	<0.6a	<0.6	7
Test Area North	0.83a	<0.6–1.6	16	—	—	—	—	—	—	—	—	—
Experimental Breeder Reactor II	0.83a	<0.6–3.3	16	—	—	—	—	—	—	—	—	—
Auxilary Reactor Area	<0.6a	<0.6	4	—	—	—	—	—	—	—	—	—
Naval Reactors Facility	<0.6a	—	4	—	—	—	—	—	—	—	—	—
Big South Butte	—	—	—	0.86ab	<0.6–2.2	17	—	—	—	—	—	—
Diversion	—	—	—	0.64c	<0.6–1.2	16	—	—	—	—	—	—
Field Station	—	—	—	1.11abc	<0.6–4.8	12	—	—	—	—	—	—
Mud Lake	—	—	—	0.81abc	<0.6–1.6	11	—	—	—	—	—	—

[1] Concentration values in each column not followed by the same letter are different.

TABLE 3
RADIONUCLIDES OTHER THAN CESIUM–137 IN MOURNING DOVE TISSUES 1974–1977

	Test Reactor Area				Idaho Chemical Processing Plant			
Radionuclide	Muscle % occurrence	(N = 50) Max. concentration pCi/g	GI % occurrence	(N = 50) Max. concentration pCi/g	Muscle % occurrence	(N = 50) Max. concentration pCi/g	GI % occurrence	(N = 50) Max. concentration pCi/g
Cesium–134	24	19	20	39.5	11	0.7	9	9.5
Iodine–131	4	1.8	22	87	—	—	3	15
Cobalt—60	26	2.2	34	227	11	8.3	9	1.2
Chromium–51	2	139	34	2620	6	0.5	3	27
Lanthanum–140	—	—	8	3.1	—	—	—	—
Cerium–141	—	—	4	37	—	—	—	—
Cerium–144	—	—	6	68.7	—	—	—	—
Ruthenium–103	—	—	2	0.9	—	—	—	—
Ruthenium–106	—	—	—	—	—	—	3	54
Manganese–54	—	—	2	8.6	—	—	—	—
Cobalt–57	—	—	2	0.3	—	—	—	—
Cobalt–58	—	—	2	0.5	—	—	—	—
Niobium–95	2	0.2	6	47	—	—	3	0.6
Zirconium–95	—	—	8	38.1	—	—	—	—
Selenium–75	4	6.5	8	10.5	—	—	—	—
Cesium–132	2	89.5	—	—	—	—	—	—
Hafnium–181	—	—	2	17.4	—	—	—	—
Zinc–65	—	—	2	21.5	—	—	—	—
Antimony–125	—	—	2	1.1	—	—	3	4.8
Barium–140	—	—	4	5.0	—	—	—	—

significantly ($P < 0.005$) different among areas (Table 1). The doves which contained significantly more ^{137}Cs in muscle tissues than control birds were from the TRA and the ICPP. The highest muscle concentration, 171 pCi/g, occurred in a bird collected in the TRA. The highest concentration of ^{137}Cs in a dove collected near the ICPP was 11.6 pCi/g. Birds collected near the RWMC, TAN, EBR-II, ARA and NRF contained ^{137}Cs concentrations similar to that in control birds. The ^{137}Cs concentrations in birds collected near the TRA and the ICPP were variable (Table 1). Birds with non-detectable ^{137}Cs concentrations were collected from both areas during each year of the study. The highest ^{137}Cs concentration in muscle from areas other than these two areas was 2.0 pCi/g and occurred in a dove collected from the background or control locations. The annual average ^{137}Cs in tissues of doves collected near the ICPP and the TRA also varied between years. However, only the data at the ICPP were significantly different between years.

Cesium-137 concentrations in dove gastrointestinal tracts were signifi-

TABLE 4

INTERNAL RADIATION DOSE RATES TO MOURNING DOVES FROM CESIUM–137 IN MUSCLE FROM 1974–1977 RADIATION DOSE (MRAD[1]/DAY)

Collection site	1974		1975		1976		1977	
	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$	Range
Test Reactor Area	0.03	<0.01–0.13	0.08	<0.01–0.45	0.03	0.02–0.04	0.30	<0.01–3.24
Idaho Chemical Processing Plant	0.06	<0.01–0.22	0.02	<0.01–0.03	0.04	0.01–0.1	—	—
Radioactive Waste Management Complex	0.01	<0.01–0.02	0.01	<0.01–0.02	—	—	—	—
Control	0.01	<0.01–0.02	0.02	<0.01–0.04	0.01	—	—	—

[1] mrad = 10^3 rad, a rad is a measurement of absorbed radiation dose.

cantly different ($P < 0.05$) among areas during 1974 and 1975 (Table 2). Gastrointestinal tracts of the doves collected near the ICPP and the TRA were significantly higher than those of the control birds or of the birds from other on-site areas. The highest ^{137}Cs concentration in the GI tracts was from the TRA (430 pCi/g). The highest concentration in ICPP gastrointestinal tissues was 139 pCi/g. The highest ^{137}Cs concentration in gastrointestinal tracts from areas other than ICPP and TRA was 7 pCi/g and occurred in a control bird.

Twenty radionuclides other than ^{137}Cs were detected in muscle and GI tracts of doves from the TRA and the ICPP during the 4-year study (Table 3). In comparison, only three radionuclides other than ^{137}Cs were detected in tissues of control doves. Chromium-51 occurred in one control GI tract at a concentration of 11 pCi/g. Cobalt-60 and ^{181}Hf each occurred in one control GI tract at concentrations less than twice the minimum detectable concentration.

Five radionuclides, ^{60}Co, ^{103}Ru, ^{106}Ru, ^{54}Mn and ^{125}Sb, occurred in seven dove tissues at locations on the INEL Site other than the TRA and the ICPP. Of these five radionuclides, only ^{103}Ru was detected in 1800 ml samples of rumen contents from off-site pronghorn antelope (*Antilocapra americana*) during the same period as this study (Markham et al. 1982). Therefore, at least four of these radionuclides in doves from other INEL locations likely resulted from INEL atmospheric or liquid discharges. The concentrations in the seven GI tract and muscle samples were less than twice the minimum detectable concentration for each radionuclide.

Dose rates to Mourning Doves from radionuclides deposited in the muscle ranged from <0.1–3.2 mrad/day (Table 4). Birds from TRA received

the highest doses in 1975 and 1977. ICPP birds had the highest doses in 1974 and 1976. The maximum dose received was by a TRA bird in 1977.

The maximum radiation dose commitment from ^{137}Cs to a person who might consume muscle tissue of a dove was 0.3 mrem. The average calculated dose for consuming doves from the TRA and the ICPP was 0.01 mrem. The other radionuclides present in dove tissues would provide an insignificant dose to people consuming dove tissues because of their low occurrence in tissues and/or their relatively low energy gamma rays and low concentration as compared to ^{137}Cs.

DISCUSSION

Mourning Doves collected at the Test Reactor Area and the Idaho Chemical Processing Plant generally contained higher ^{137}Cs concentrations and had a higher occurrence of other radionuclides than did birds from the control area and other INEL facilities. The ICPP releases over 99% of the particulate radionuclide emissions of INEL facilities. Similarly, the TRA radioactive leaching ponds have received approximately 85% of the total radioactive waste water discharged to the lithosphere from all INEL facilities (Millard et al. 1976). Therefore, the two primary sources of contamination for doves on the INEL Site were atmospheric effluents associated with nuclear fuel reprocessing and liquid effluents associated with test reactors. The storage of solid radioactive waste beneath the soil surface at the RWMC apparently did not contribute to the body burden of radionuclides in doves. Other on-site nuclear facilities such as reactors and nuclear fuel handling and examination facilities were not sources of contamination for these birds either. The ^{137}Cs concentrations in control birds were likely due to worldwide fallout from previous atmospheric testing of nuclear weapons.

A variety of wildlife, including 94 bird species, have been observed at the TRA radioactive leaching ponds (Halford and Millard 1978). Many of these birds either feed or drink at these ponds. Waterfowl collected from the TRA ponds during the same years as this study contained average ^{137}Cs muscle concentrations that were over 150 times larger than the average concentrations in Mourning Doves (Halford et al. 1981). Raptors within 3.5 km of the TRA apparently obtained a portion of their prey near the leaching ponds. Raptor nestlings located within 0.2 km of the ponds contained wholebody radionuclide concentrations which ranged from 1.3–87 pCi/g (Craig et al. 1979). Adult Barn Swallows (*Hirundo rustica*) nesting near the TRA radioactive leaching ponds contained average wholebody ^{137}Cs concentrations of 90 pCi/g and also contained higher concentrations of several other radionuclides than did doves (Millard et al. 1978). Sage Grouse (*Centrocercus urophasianus*) also have been studied at the TRA

pond and contained concentrations of ^{137}Cs which were similar to those occurring in doves (Connelly and Markham, in press).

Based on our observations, Mourning Doves at the TRA ponds primarily drink water in this area, but do not feed extensively. Therefore, their concentrations of ^{137}Cs were lower than Barn Swallows, waterfowl and raptors which also feed in the area. Raptors apparently obtained their radionuclide body burden from prey captured near the TRA ponds (Craig et al. 1979). Barn Swallows feed on emerging insects from the pond (Millard et al. 1978) and waterfowl feed on pond flora and fauna (Halford et al. 1981). Sage Grouse occasionally feed on littoral vegetation and some likely drink at these ponds. The ^{137}Cs concentrations in the water at the TRA ponds are factors of 80–30,000 times less than concentrations in flora and fauna in the ponds (Millard et al. 1978).

We have observed doves feeding and obtaining grit in and around the ICPP area. Raptors, which also likely obtained a portion of their diet from the ICPP area, generally contained lower radionuclide concentrations than doves collected near the ICPP (Craig et al. 1979). Muscle from pronghorn antelope collected 1974–1976 within 10 km of the ICPP averaged 0.3 pCi $^{137}Cs/g$ (Markham et al. 1982), which was lower than the concentrations in ICPP doves. However, the pronghorn and raptor samples were obtained over a much larger area than were the doves.

Studies by our laboratory indicate that ^{137}Cs concentrations in soil surrounding the ICPP rapidly decrease with distance. Therefore, the relative locations of feeding activities in the ICPP area would affect ^{137}Cs concentrations. Also, part of the variability of ^{137}Cs in dove tissues was probably due to the variable amount of time doves spent drinking at TRA or feeding near the ICPP. Water was available at other locations at the ICPP and TRA, so doves could spend considerable periods of time at either facility without having to drink water from the radioactive leaching ponds. The differences in regularity of individuals drinking at the radioactive leaching pond also likely affected the variability of ^{137}Cs concentrations.

The average ^{137}Cs muscle concentrations in doves at the ICPP during 1974, 1975 and 1976 were 3.24, 0.84 and 1.98 pCi/g, respectively. The ICPP released 6.7, 0.6 and 0.1 Ci of ^{137}Cs/year in its atmospheric effluents for 1974, 1975 and 1976, respectively. During 1975, additional filters were added to the filter system at the ICPP. Thus, the total atmospheric releases of ^{137}Cs in 1975 and 1976 were reduced over those of 1974. Subsequently, the ^{137}Cs concentrations in dove tissues from the ICPP area were reduced.

Radiation dose rates received by doves ingesting radionuclides were similar to those received by raptors nesting near TRA and ICPP (Craig et al. 1979). Deer mice (*Peromyscus maniculatus*) from the TRA received

average internal dose rates of 5 mrem/day (Halford and Markham 1978), about 15 times higher than the highest mean internal dose rate to doves. Young Barn Swallows at TRA received average daily doses of 220 mrad (Millard et al. 1978), over 700 times the doses received by Mourning Doves. All of the previously mentioned studies have found no radiation-induced effects from the ingestion of radionuclides. The doses received by doves in this study (Table 4) are low compared to doses cited in these previous studies and therefore would not be expected to produce any radiation hazard to the birds.

Cobalt-58, ^{51}Cr and ^{131}I were present in three doves collected at ICPP. These radionuclides do not normally occur in ICPP atmospheric effluents (White 1978) since nuclear fuels reprocessed at the ICPP have been aged sufficiently so that these short-lived isotopes have decayed. Therefore, the presence of these radionuclides in these three ICPP birds indicate that these birds were present at the TRA radioactive leaching ponds at some earlier date. Although the ICPP and TRA sites are only 3 km apart, little mixing of these birds apparently occurred.

Similarly, there was no evidence that large numbers of doves became contaminated and moved to other portions of the INEL Site. Since ^{137}Cs is a ubiquitous fallout product from previous above-ground nuclear bomb tests, its presence or absence could not be used to determine whether doves had visited TRA prior to collection. However, 20 radionuclides other than ^{137}Cs that do not normally occur in worldwide fallout were detected in muscle and GI tract samples from TRA birds and these could be used to determine their past presence at TRA. Only 4 of 124 doves collected on or near the site at locations other than ICPP and TRA contained radionuclides that could be traced to the TRA radioactive leaching ponds.

The INEL Site is closed to hunting so no Mourning Doves are legally harvested there. However, doves at TRA and ICPP are available for harvest by sportsmen during the September hunting seasons when the doves frequently fly offsite to feed on wheat (Trost et al. 1976) or migrate from the INEL Site. The potential radiation dose equivalent to a human eating a dove, containing the maximum ^{137}Cs concentration observed in muscle tissue in this study, was only 0.3 mrem. In perspective, this dose is approximately 0.3% of the average 117 mrem/year radiation dose equivalent received by humans in the INEL area from naturally occurring external radiation (U.S. Dept. Energy 1979) and 2% of the 17 mrem people received from ^{40}K, a naturally occurring radionuclide in the body (Klement et al. 1972). The maximum permissible wholebody dose commitment to an individual in the general population, as established by the I.C.R.P. (1959) and the U.S. Dept. Energy (1977), is 500 mrem/year. The radiation dose to humans from consuming doves would be negligible. Waterfowl from the

TRA which contained higher concentrations than doves and had greater mass have also been shown not to be a hazard to people consuming them (Halford et al. 1981). Although not determined, the biological half-life (the time necessary for one-half of the cesium to be eliminated from the body) for doves is probably similar to the 11-day average for Mallards (*Anas platyrhynchos*) (Halford et al., unpubl.), the 6-day average for Wood Ducks (*Aix sponsa*) (Fendley et al. 1977) and the 6.7-day half-life reported for Blue Jays (*Cyanocitta cristata*) (Levy 1975). Therefore, it is likely that the doves would quickly eliminate the ^{137}Cs once they migrated from the source of contamination.

SUMMARY

Tissues from 252 Mourning Doves (*Zenaida macroura*) were collected near seven different types of nuclear facilities and four other locations on and near the Idaho National Engineering Laboratory Site in southeastern Idaho and analyzed for gamma emitting radionuclides. Cesium-137 was the only radionuclide commonly present in tissues from all locations. Only Mourning Doves collected at the Test Reactor Area (TRA) and the Idaho Chemical Processing Plant (ICPP) contained higher concentrations of ^{137}Cs than control birds. Twenty radionuclides other than ^{137}Cs were detected in samples from TRA and ICPP but their frequency of occurrence and concentrations were much lower than for ^{137}Cs. Cesium-137 and other radionuclides in doves from the ICPP had their origin as atmospheric effluents from the ICPP while radionuclides in the TRA birds originated from radioactive leaching ponds. There was no evidence the doves became contaminated at TRA and moved to other locations as only four of the 124 doves collected at other locations on and near the INEL Site contained radionuclides that originated from TRA. Cesium-137 in muscle tissues would contribute a negligible potential radiation dose to the birds or to humans consuming the doves.

ACKNOWLEDGMENTS

This research was funded by the Division of Biomedical and Environmental Research, U.S. Dept. Energy, and is a contribution from the Idaho National Engineering Laboratory Radioecology Program. We thank J. S. Morton for analytical assistance, and J. B. Millard, J. DeHerrera, R. Hawk and S. Martin for field assistance.

LITERATURE CITED

Arthur, W. J. and O. D. Markham. 1978. Ecology studies at the Idaho National Engineering Laboratory Radioactive Waste Management Complex. Pp. 74–92 *in* Ecological studies on the Idaho National Engineering Laboratory Site 1978 progress report, IDO-12087 (O. D. Markham, ed.), Natl. Tech. Info. Serv., Springfield, Virginia.

Connelly, J. W. and O. D. Markham. 1982. Movements and radionuclide concentrations of Sage Grouse in southeastern Idaho. J. Wildl. Manage. In press.

Craig, T. H., D. K. Halford and O. D. Markham. 1979. Radionuclide concentrations in nesting raptors near nuclear facilities. Wilson Bull. 91:72–77.

Fendley, T. T., M. N. Manlove and I. L. Brisbin, Jr. 1977. The accumulation and elimination of radiocesium by naturally contaminated Wood Ducks. Health Phys. 32:415–422.

Halford, D. K. and O. D. Markham. 1978. Radiation dosimetry of small mammals inhabiting a liquid radioactive waste disposal area. Ecology 59:1047–1054.

——— and J. B. Millard. 1978. Vertebrate fauna of a radioactive leaching pond complex in southeastern Idaho. Great Basin Nat. 38:64–70.

———, J. B. Millard and O. D. Markham. 1981. Radionuclide concentrations in waterfowl using a liquid radioactive waste disposal area and the potential radiation dose to man. Health Phys. 40:173–181.

Harniss. R. O. and N. E. West. 1973. Vegetation patterns of the National Reactor Testing Station, southeastern Idaho. Northwest Sci. 47:30–43.

Hollander, M. and D. A. Wolfe. 1973. Nonparametric statistical methods. John Wiley and Sons, New York, New York.

International Commission on Radiological Protection. 1959. Permissible doses for internal radiation, Publ. 2. Pergamon Press, London, England.

———. 1968. Evaluation of radiation doses to body tissues from internal contamination due to occupation exposure, Publ. 10. Pergamon Press, London, England.

Klement, A. W., Jr., C. R. Miller, R. P. Minx and B. Schleien. 1972. Estimates of ionizing radiation doses in the United States. 1960. ORP/CSD 72–1. U.S. Environ. Protection Agency, Rockville, Maryland.

Levy, C. K. 1975. Avian radioecology on a nuclear power station site. Tech. Progr. Rept. Manomet Bird Observatory, Manomet, Massachusetts.

Markham, O. D., D. K. Halford, R. E. Autenrieth and R. L. Dickson. 1982. Radionuclides in pronghorn resulting from nuclear fuel reprocessing and worldwide fallout. J. Wildl. Manage. 46:30–42.

McBride, R., N. R. French, A. H. Dahl and J. E. Detmer. 1978. Vegetation types and surface soils of the Idaho National Engineering Laboratory Site, IDO-12084. Natl. Tech. Info. Serv., Springfield, Virginia.

Millard, J. B., F. W. Whicker and O. D. Markham. 1976. An ecological study of the Test Reactor Area radioactive leaching ponds. Pp. 17–18 *in* 1975 progress report Idaho Natl. Engin. Lab. Site radioecology-ecology program, IDO-12080. Natl. Tech. Info. Serv., Springfield, Virginia.

———, ——— and ———. 1978. Barn Swallows nesting near radioactive leaching ponds in southeastern Idaho. Pp. 1–14 *in* Ecological studies on the Idaho Natl. Engin. Lab. Site 1978 progress report, IDO-12087. Natl. Tech. Info. Serv., Springfield, Virginia.

Reynolds, T. D. and C. H. Trost. 1981. Grazing, crested wheatgrass, and bird populations in southeastern Idaho. Northwest Sci. 55:225–234.

Trost, C. H., O. D. Markham and J. DeHerrera. 1976. Food and habits of doves on the INEL Site. Pp. 7–9 *in* Summaries of the Idaho National Engineering Laboratory Site ecological information meeting, IDO-12079 (O. D. Markham, ed.). Natl. Tech. Info. Serv., Springfield, Virginia.

U.S. Department of Energy. 1977. Standards of radiation protection. U.S. Energy Research and Development Administration Manual Chapter 0524, Washington, D.C.

U.S. Department of Energy. 1979. 1978 Environmental monitoring program report for Idaho Natl. Engin. Lab. Site, IDO-12082. Natl. Tech. Info. Serv., Springfield, Virginia.

White, S. S. 1978. Idaho National Engineering Laboratory radioactive waste management information 1977 summary and record-to-date, IDO-10054(77).

RADIOLOGICAL AND ENVIRONMENTAL SCIENCES LABORATORY, U.S. DEPT. ENERGY, IDAHO FALLS, IDAHO 83401. ACCEPTED 30 JUNE 1981.

GENERAL NOTES

Wilson Bull., 94(2), 1982, pp. 198–201

Great Blue Heron eggshell thickness at Oregon estuaries.—The thickness of eggshells of Pacific coast Great Blue Herons (*Ardea herodias*) has decreased since the pesticide era began in California (Wilburn, Lincoln Great Blue Heron Rookery Study, 1970–1971, California Dept. Fish Game, Spec. Wildl. Invest., 1972; Faber et al., Environ. Pollut. 3:111–122, 1972; Ives, California Dept. Fish Game, Spec. Wildl. Invest., Admin. Rept. No. 72–9, 1972) and in inland Oregon (Blus et al., Murrelet 61:63–71, 1980). Herein, I report eggshell thicknesses at eight colonies near four Oregon estuaries. I also document yearly and intraseasonal variation in thickness. These latter aspects have not been previously examined for any herons, and yearly variation has been measured only in Brown Pelicans (*Pelecanus occidentalis*) (Mendenhall and Prouty, Proc. Colonial Waterbird Group 2:65–70, 1978; Schreiber, Bioscience 30:742–747, 1980).

Study area and methods.—I designated heron colonies by the estuary name and the cardinal compass direction of the heronry from the estuary. The four study estuaries (colony names in parentheses) were the Yaquina (Yaquina-N, -S and -E), the Alsea (Alsea-S), the Coos (Coos-N, -W and -S) and the Coquille (Coquille-N). Yaquina-E and Coquille-N were mapped as the Mill Creek and Bandon colonies, respectively, in Werschkul et al. (Murrelet 58:7–12, 1977); and the other colonies are mapped in Bayer and McMahon (Murrelet, In Press). Chemical contaminants that may have influenced eggshell thickness could have resulted from agricultural or forestry practices at all four estuaries, and/or from pulp and paper plants at the Yaquina and Coos estuaries.

Eggshells dropped from the nest to the ground by the parents after hatching or through accident were collected during visits to Yaquina-S from 1973–1979, to Coquille-N and Coos-N, -W and -S in 1975, to Alsea-S in 1975 and 1976, and to Yaquina-N and -E in 1979.

Eggshells were rinsed after collection to remove debris; those collected from 1973–1978 were dried at room temperature until June 1979, when their thickness was measured. Eggshells from 1979 were dried at room temperature for at least 74 days before measurement. If the end of the shell had been chipped away it was regarded as one from which a young bird had hatched; all other eggshells were considered to be from unhatched eggs (see Faber et al. 1972).

Shell thickness was measured with a Starrett micrometer fitted with a ball to measure curved surfaces. I calculated a mean from thickness measurements made at three sites along the equator where the shell membrane was still attached to the shell.

Results and discussion.—The mean annual percentage of unhatched eggshells at Yaquina-S was 7.8% (range = 7–10%, N = 6) and was ≤8% at Coquille-N, Coos-W and Coos-S. However, at Coos-N and Alsea-S more eggshells were unhatched (16 and 17%, respectively); most of the unhatched eggshells at these two colonies were found a few days after high winds. The higher proportion of unhatched eggs at these two colonies, which were more exposed to wind than other colonies, probably resulted from the wind destroying nests or blowing eggs out of nests rather than from pesticides or eggshell thinning. I did not find at any colony shells that appeared crushed or dented, and only at Yaquina-E in 1979 were eggs found that broke when picked up. There was a nonsignificant correlation ($r = -0.33$, df = 11, $P > 0.10$) between the proportion of unhatched eggshells and mean hatched eggshell thickness. In contrast, a much higher percentage (29–67%) of unhatched shells was found in some California colonies (Page, Sec. Prog. Rept., San Joaquin River Rookery Study, 1971, California Dept. Fish Game, Spec. Wildl. Invest., 1971; Faber et al. 1972; Wilburn 1972).

The mean thickness of hatched eggshells was significantly less than the pre-1947, pre-

Table 1

Great Blue Heron Pre-1947 Whole Egg and Post-1972 Hatched Eggshell Thickness

Area		Eggshell thickness (mm) N	$\bar{x} \pm$ SD	Range	% change from pre-1947 mean[c]
Pacific northwest	pre-1947	186[a]	0.3861 ± 0.021[a]	0.290–0.437[b]	—
Yaquina-N and -E	1979	20	0.3240 ± 0.015	0.285–0.348	−16.1
Yaquina-S	1973	70	0.3467 ± 0.025	0.252–0.391	−10.2
Yaquina-S	1974	50	0.3520 ± 0.027	0.279–0.391	−8.8
Yaquina-S	1975	46	0.3542 ± 0.021	0.300–0.403	−8.3
Yaquina-S	1976	128	0.3562 ± 0.024	0.277–0.394	−7.7
Yaquina-S	1977	86	0.3542 ± 0.024	0.300–0.414	−8.3
Yaquina-S	1978	41	0.3759 ± 0.018	0.338–0.424	−2.6
Yaquina-S	1979	63	0.3362 ± 0.023	0.264–0.396	−12.9
Alsea-S	1975	36	0.3466 ± 0.029	0.227–0.417	−10.2
Coos-N	1975	61	0.3549 ± 0.023	0.315–0.406	−8.1
Coos-W	1975	42	0.3529 ± 0.019	0.300–0.381	−8.6
Coos-S	1975	35	0.3597 ± 0.023	0.269–0.396	−6.8
Coquille-N	1975	36	0.3490 ± 0.020	0.300–0.378	−9.6

[a] From Anderson and Hickey (pp. 514–540 *in* Proc. XV Int. Ornithol. Congr., K. H. Voous, ed., 1972) and H. M. Ohlendorf (pers. comm.) for whole eggs.
[b] From H. M. Ohlendorf (pers. comm.) for whole eggs collected at nest.
[c] Differences significant at $P < 0.05$, df ≥ 204, means compared using student's t-test.

pesticide era thickness in all years (Table 1). However, there was yearly variation at Yaquina-S with mean thickness relatively stable from 1973–1977, increasing in 1978, and decreasing to a minimum for all years in 1979 (Table 1). Yaquina-S means were significantly different among all years (1973–1979) ($F = 12.22$; df = 6, 477; $P < 0.01$).

Eggshell thickness sometimes varied among colonies. In 1975, the means for the Coos colonies and Yaquina-S did not differ significantly from each other ($F = 0.42$; df = 3, 181; $P > 0.05$), but the combined mean of the Coos colonies and the Yaquina-S colony differed significantly ($F = 3.05$; df = 2, 254; $P < 0.05$) from the means of Alsea-S and Coquille-N (also see Table 1). In 1979, Yaquina-N and -E mean thickness was significantly less ($F = 6.00$; df = 1, 81; $P < 0.05$) than the mean for Yaquina-S, but these means were lower than all means in previous years (Table 1).

Eggshell thicknesses did not show consistent patterns of increase or decrease within a breeding season (Fig. 1). The mean thickness of eggshells for any particular date was within 4.7% of the mean for the entire breeding season, but means for dates within a season varied by as much as 7.3% (Fig. 1). Mean thickness for a given date within a season was not significantly different from others in 1976 ($F = 1.25$; df = 6, 121; $P > 0.05$) or 1979 ($F = 0.70$; df = 6, 56; $P > 0.05$) but were in 1977 ($F = 8.33$; df = 3, 80; $P < 0.01$). Therefore, differences between pre-1947 and current eggshell thicknesses or the actual mean thickness during a breeding season may either be obscured or biased by collections of eggshells from a single visit.

I found that the mean thickness for hatched eggshells from all colonies ($\bar{x} = 0.3518 \pm 0.024$ mm, range = 0.252–0.424 mm, N = 720) was significantly greater ($t = 4.60$, df = 759, $P < 0.01$) than for unhatched shells ($\bar{x} = 0.3324 \pm 0.430$ mm, range = 0.229–0.389 mm,

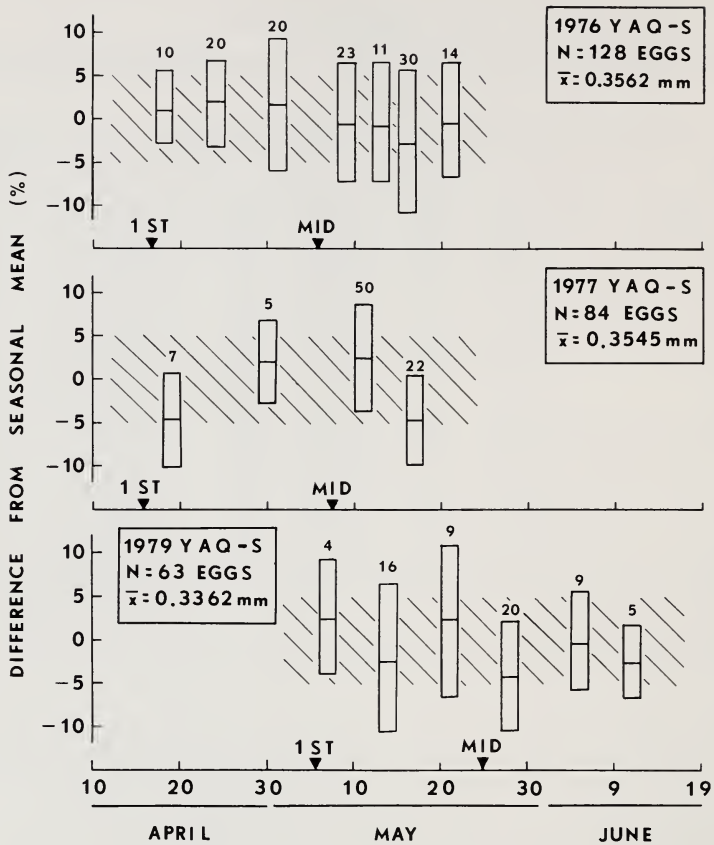


FIG. 1. Percent difference of hatched eggshell mean thickness/visit (horizontal line) and standard deviation of mean/visit (vertical bar) from hatched eggshell mean thickness/breeding season ($\bar{x}$ in yearly legend) at Yaquina-S. Dates of first (1ST) and 50% (MID) hatching from Bayer and McMahon (In Press). Number of eggshells/visit is above vertical bar. Crosshatching represents thicknesses within 5% of breeding season mean.

N = 41). Both means were significantly thinner than the pre-1947 mean given in Table 1 (hatched: 8.8% less, $t = 16.92$, df = 904, $P < 0.01$; unhatched: 13.9% less, $t = 11.25$, df = 225, $P < 0.01$). Similarly, Faber et al. (1972) and Ives (1972) showed that hatched eggshells of Great Blue Herons were thinner than pre-1947 eggshells (7.8 and 10.6%, respectively) and that hatched eggshells were generally thicker than unhatched eggshells. The thinnest eggs may have had the highest probability of not hatching because of behavioral abnormalities of the parents (e.g., egg piercing or rejection, see Milstein et al., Ardea 58:171–257, 1970; Cooke et al., Environ. Pollut. 11:59–84, 1976) or because of decreased viability resulting from increased pesticide loads (Cooke et al. 1976). In fact, the difference in thickness between hatched and unhatched eggshells may have been even greater when eggs were first laid, since incubation may typically reduce thickness by about 8% in several species (Kreitz-

er, Poult. Sci. 51:1764–1765, 1972; Rothstein, Wilson Bull. 84:469–474, 1972; Capen, Wilson Bull. 89:99–106, 1977; Pulliainen and Marjakangas, Ornis. Scand., Fenn. 57:65–70, 1980; but see Ohlendorf et al., U.S.D.I., Fish and Wildl. Serv., Spec. Sci. Rept. Wildl. No. 216, 1979). However, incubation thinning is apparently not equal for all eggs of a species (Capen 1977).

Unfortunately, pre-1947 Great Blue Heron eggshells were probably not incubated long, so a comparison between pre-1947 and current eggshells dropped from the nest will not be rigorous until there are data available concerning thinning during incubation of eggshells of *A. herodias*. Nevertheless, using 8% as a standard of incubation thinning (Pulliainen and Marjakangas 1980), I estimate that much of the difference I found between pre-1947 and current-hatched eggshell thicknesses may result from this form of thinning. However, the yearly variation in thicknesses and the variation among colonies (Table 1) indicates that incubation thinning is not the only cause of current eggshells being thinner than those prior to 1947. In any case, I found that the degree of thinning of current-hatched eggshells compared with pre-1947 eggshells was generally less than the 15–20% thinning associated with declining bird populations (Anderson and Hickey 1972).

Research design.—To make collections of eggs yielding the most information one should collect both whole eggs and dropped eggshells. Whole eggs are necessary for the determination of pesticide or heavy metal levels. Collecting eggs at the same stage of incubation as represented by pre-1947 eggshells (generally shortly after being laid [see Anderson and Hickey, Wilson Bull. 82:14–28, 1970]) is required to compare present day and pre-1947 shells. However, collecting eggs that have fallen from the nest is often the only practical way to collect eggshells in inaccessible colonies, e.g., at Yaquina-S where nests are 20–30 m above the ground, or to determine the thickness of shells of hatched or unhatched eggs and the proportion of unhatched eggs. Furthermore, collection of eggshells from the ground minimizes disturbance to nesting birds while maximizing the proportion of the colony's eggshells sampled.

Acknowledgments.—I am grateful to V. Weber and E. Thayer of the Oregon State University Marine Science Center for the loan of a micrometer, to H. M. Ohlendorf for providing unpublished data and to E. McMahon for collecting some of the eggshells from the Coos and Coquille colonies. H. M. Ohlendorf, L. Kiff, E. E. Klaas, G. A. Fox and L. J. Blus critically read earlier drafts of this paper.—Range D. Bayer, *423 SW 9th, Newport, Oregon 97365.* *Accepted 13 May 1981.*

Wilson Bull., 94(2), 1982, pp. 201–206

Nesting phenology of the Double-crested Cormorant.—The Double-crested Cormorant (*Phalacrocorax auritus*) is a locally common, colonially nesting bird of the lakes, rivers and estuaries of much of North America. The nesting cycle of the cormorant is decidedly seasonal over much of this range. Published accounts indicate spring–sumer nesting to be the rule (e.g., Bent, U.S. Natl. Mus. Bull. 121, 1922; Palmer, Handbook of North American Birds, Yale Univ. Press, New Haven, Connecticut, 1962; Weseloh et al., Proc. Colonial Waterbird Group 2:10–18, 1977). A few data suggest that cormorants may have a longer reproductive season in Florida, where nesting has been reported as early as December and as late as October (Palmer 1962). In this note, we describe the nesting cycle and other population characteristics of cormorants in southern Florida.

Methods.—Cormorant colonies were located and the number of nests were counted to

FIG. 1. Map of South Florida showing locations of Double-crested Cormorant colonies, 1977–78. Major colonies (>100 nests) are indicated by double symbols and numbers corresponding to Table 1. Single symbols show location of minor colonies. Colonies are divided geographically into eastern Florida Bay (open squares), southern Florida Bay (closed circles), western Florida Bay (closed squares), Gulf coast (open circles) and inland (x).

about ±10% during monthly aerial reconnaissance by fixed-wing aircraft or helicopters. The area of southern Florida covered included the southern Florida Gulf coast and Florida Bay (Fig. 1). Data reported were collected from May 1977–May 1978. Less accurate information collected in the succeeding year indicated that the 1977–78 season was not atypical.

Results.—During 1977–78, cormorants nested in 30 locations on the study area (Fig. 1). Three colonies were along the Gulf coast, seven in western Florida Bay, 12 in southern Florida Bay, six in eastern Florida Bay and two inland. The noncoastal colonies were on mangrove islands in an estuarine bay and in a brackish-water lake (Fig. 1). During the study year, 4700 nests were found in the study area. They were dispersed among a few large and many smaller colonies, with over 70% of the colonies containing fewer than 100 nests.

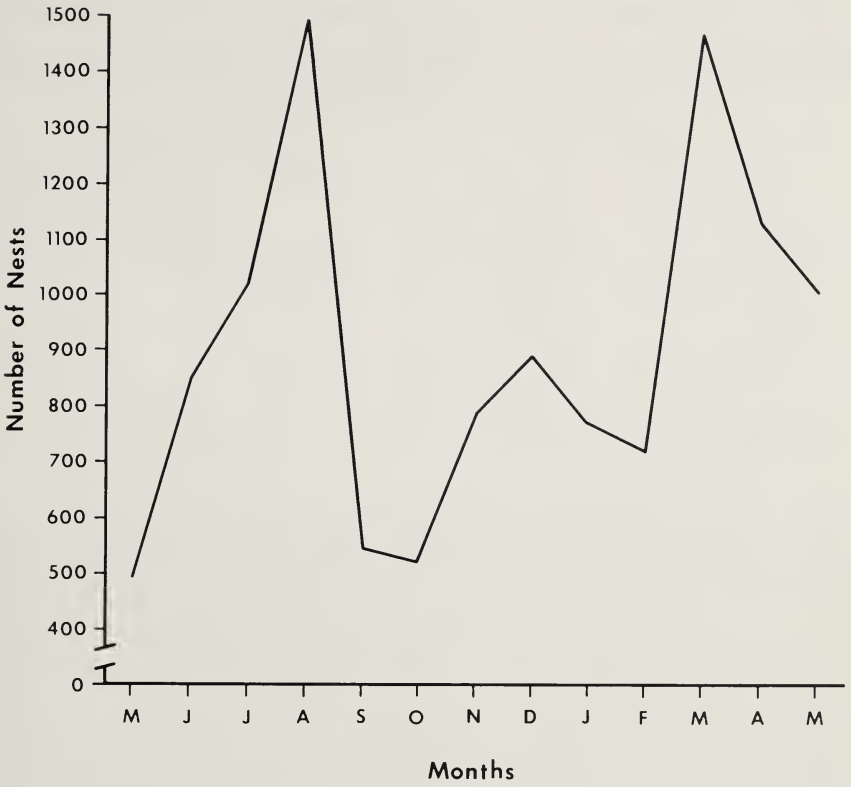


FIG. 2. Number of Double-crested Cormorant nests found in south Florida each month from May 1977–May 1978.

Seventy-three percent of the nests were concentrated in eight colonies, each having more than 100 nests (Table 1). These colonies were located mostly in western and southern Florida Bay (Fig. 1).

Cormorants nested year-round in southern Florida during the study period (Fig. 2). Although some colony sites were active for only part of the year, cormorants nested in every month at colonies at Frank Key and at Sandy Key in western Florida Bay. Numbers of active nests at a specific time varied from 490 in May 1977 to 1500 in August 1977 (Fig. 2). Three peaks of nesting activity occurred within the year (Fig. 3). The winter peak (Nov.–Jan.) was considerably smaller than the summer (June–Aug.) or spring (Mar.–May) peaks.

Cormorants nesting in western Florida Bay accounted for most of the birds found in winter and spring (Fig. 3). Birds nested on the Gulf coast in summer. Most nests in fall were in southern Florida Bay. Regional variation can be seen in the timing of nesting among major colonies (Table 1). The number of summer nesting birds peaked first in colonies on the west coast in June, followed by colonies in southern Florida Bay in July and August. In spring, nesting peaked first in western Florida Bay in March and then in southern Florida Bay in May.

Discussion.—The Double-crested Cormorant has undergone long-term decreases in many

Table 1

Peak Numbers of Double-crested Cormorants Nesting at Major Colony Sites in South Florida, May 1977–May 1978

Colony name	Area	Peak number (month)		
		Summer	Winter	Spring
1.[a] Sandy Key	western Florida Bay	—	300 (Dec.)	1500 (Mar.)
2. Frank Key	western Florida Bay	200 (July)	300 (Dec.)	400 (Mar.)
3. Upper Arsnicker Key	southern Florida Bay	350 (Aug.)	—	—
4. Chokoloskee	western Gulf Coast	230 (June)	—	—
5. Palm Key	western Florida Bay	—	—	200 (Mar.)
6. West Buchanan Key	southern Florida Bay	175 (Aug.)	—	150 (May)
7. Green Mangrove Key	southern Florida Bay	170 (Aug.)	—	—
8. East Buchanan Key	southern Florida Bay	130 (Aug.)	150 (Jan.)	—

[a] Numbers indicate locations of colonies on Fig. 1.

areas of North America, especially inland populations, (Anderson and Hamerstrom, Passenger Pigeon 29:3–15, 1967; Mitchell, Am. Birds 29:927–930, 1975; Thompson, Proc. Colonial Waterbird Group 2:26–37, 1977). Recently, cormorant populations of the eastern part and interior of North America have begun to recover (Robertson, pers. comm.; Weseloh et al. 1977). During the study year, we found at least 4700 cormorant nests in south Florida. This is the best available estimate of the size of the breeding population, although some birds might have nested more than once during the year and been counted each time, or some might have reused nest-sites which were counted only once. The present survey did not include the southern Florida Keys, which held at least 4500 cormorant nests when we surveyed them in 1976. In that same year, another 650 nests occurred along the southeastern Florida coast in Biscayne Bay. If these data from 1976 were also representative of the situation in 1977–78, we can estimate the total population in south Florida to be about 20,000 birds.

Double-crested Cormorants are primarily coastal in southern Florida (Fig. 1; Owre, Ornithol. Monogr. 6, 1967). Nesting inland is rare, such as the few nests in the marshes of northern Everglades in the early 1970's (J. Schortemeyer, pers. comm.). Most birds occurring inland are juveniles, frequenting the limited deep-water habitats such as canals and borrow pits.

Cormorants are known to change colony sites in response to disturbance, changing environmental conditions and other factors (Palmer 1962). This may not be the rule in southern Florida, where the earliest recorded colony sites at Cuthbert Lake (Bent 1922; Howell, Florida Birdlife, Coward-McCann, New York, New York, 1932) and at Chokoloskee and Man-of-War Key (Howell 1932) were still active in 1977–78. Cuthbert Island, greatly reduced in area by a hurricane, can no longer be considered a large colony as described by Howell (1932). The six colony sites found in a census in 1974–75 (Kushlan and White, Florida Sci. 110:65–72, 1977) were all active 3 years later. Colony-site permanence, or at least slow turnover, suggests that the population is stable, perhaps because of its coastal location and probable low levels of ambient pesticide loading.

In southern Florida, Double-crested Cormorants nested year-round during the study year even at single colony sites, resembling in this other south Florida colonial water birds, such as Great Egrets (*Egretta albus*) (Kushlan and White 1977) and Great White Herons (*Ardea herodias*) (Robertson and Kushlan, pp. 414–452 *in* Environments of South Florida: Present

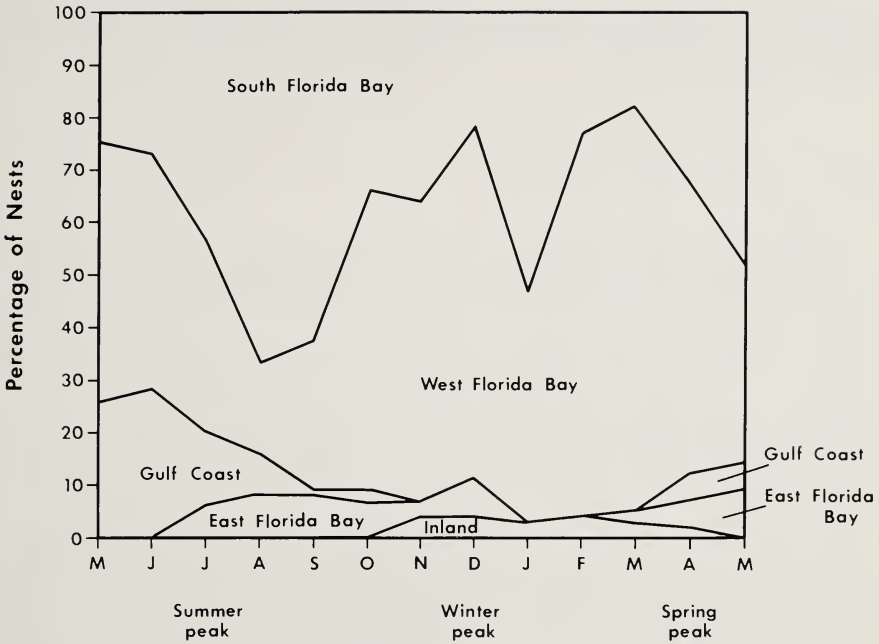


FIG. 3. Proportion of total cormorant nesting in different regions of south Florida.

and Past, Miami Geol. Soc., Miami, Florida, 1974). Possibly the subtropical environment allows exploitation of a more consistently available or consistently accessible food supply, at least during the present study period. Information from more tropical colonies in Cuba and the southern Bahamas would be of considerable comparative value in this respect. It is notable that the most seasonal of the southern Florida colonies were the most northern ones along the Gulf coast. There, nesting may be determined by sea surface temperatures, which are influenced by cool longshore currents. The single summer peak of nesting occurring in these colonies appears to be typical of cormorant colonies further north.

Variability in timing and numbers of cormorants nesting within different areas of south Florida indicates that specific areas were differentially valuable in maintaining the cormorant population. Western Florida Bay was the most productive area, as evidenced by large population size and year-round nesting. Southern Florida Bay was also productive, although somewhat more seasonal. In general, the most productive colony sites were on the outer reaches of Florida Bay where productivity was probably influenced by both bay and Gulf waters. Sampling data in this area suggest that higher populations of some forage fishes occur there than further east in Florida Bay (T. Schmidt, pers. comm.), suggesting a possible relationship of cormorant nesting population size and food supply. A sizeable population, long-term occupation of colony sites and flexibility in population nesting cycle, including year-round nesting in some locations, characterize the Double-crested Cormorant population in southern Florida.

Acknowledgments.—We thank R. Miele and A. Lussier, our pilots on the aerial surveys; we also thank J. C. Barlow, O. L. Bass, Jr., P. C. Frohring, O. T. Owre, and W. B. Robertson, Jr. for reviewing the paper.—JAMES A. KUSHLAN AND LINDA C. MCEWAN, *Na-*

tional Park Service, South Florida Research Center, P.O. Box 279, Homestead, Florida 33030. (Present address LCM: *U.S. Forest Service, Deschutes National Forest, Bend, Oregon 97701.*) *Accepted 2 Apr. 1981.*

Wilson Bull., 94(2), 1982, pp. 206–208

Replacement nesting and polyandry in the Wattled Jacana.—Although polyandry has been documented for the Bronze-winged Jacana (*Hydrophasianus chirurgus*) (Hoffman, Ornithol. Bericht 2:119–126, 1950) and Northern Jacana (*Jacana spinosa*) (Jenni and Collier, Auk 89:743–789, 1972) its occurrence in the Wattled Jacana (*J. jacana*) has been speculative (Osborne and Bourne, Condor 79:98–105, 1977). Polyandry in *J. jacana* is predicted because females are freed from parental care of the precocial young (Osborne and Bourne 1977) thus potentially enabling them to lay additional clutches (Pitelka, Holmes and MacLean, Am. Zool. 14:185–204, 1974) and to monopolize several mates (Emlen and Oring, Science 197:215–223, 1977). In this paper, I report my observations on productivity, replacement nesting and pair bonding for jacanas breeding in coastal Guyana, and describe polyandry in this species for the first time.

Study area.—Field studies were conducted on a 28 ha study plot at Burma of MARDS, Guyana, South America, from June–November 1977. MARDS is under intensive rice cultivation and experiences two wet and two dry seasons annually (Giglioli, Crop Histories and Field Investigations 1951–1957, British Guiana Rice Develop. Co. Ltd., Georgetown, Guyana, 1959). During the 1977 study period the wet season extended from May–July, the dry season from August–November. The study plot, partitioned by dikes and canals, consisted of 90% ricefields, 4% drainage ditches, 3% cattle paddocks and 3% ponds, and was surrounded by about 1600 ha of ricefields.

Productivity.—Nests were checked daily over the 6 months and their success determined. Nest and egg loss was high. Of 52 nests, only eight (15.4%) were successful in producing at least one young. Fates of the precocial young after leaving the nest were not followed. Known causes of nest and egg loss included lizards (1.9%), Long-winged Harriers (*Circus buffoni*) (5.8%), children (5.8%), grazing cattle and horses (19.2%), and harrowing and drainage of the ricefields (9.6%). Thus, natural predators accounted for 7.7% of the known nest and egg loss and human related activities for 34.6%. Thirty-five percent of the nests were lost to unknown causes, perhaps to changing water depths, and 7% were presumed deserted.

Pair bonds and replacement nesting.—Jacanas were captured by mist-net, sexed by weight (Osborne and Bourne 1977) and marked with colored plastic leg bands (identified in this paper by acronyms or capital letters, e.g., WO/O and D, respectively). Censuses of the marked population were made twice weekly from June–November to determine pair bond relationships and the frequency of replacement nesting. The existence of a pair bond between a male and female was inferred from their foraging together on the territory, territorial defense and precopulatory behavior (Osborne and Bourne 1977). Many, but not all pairs were observed during repeated copulations.

Thirty-four males and 19 females were marked. Nineteen birds (38% of the males and 31% of the females) left the study area. Twenty-one of the 34 males (61.8%) and 13 of the 19 females (68%) nested in the study area. Eight of 21 males (38%) and 2 of 13 females (15.4%) paired with unmarked mates. Nine of 11 females (81.8%) were monogamous, two (18.2%) were polyandrous.

Females responded to acts of predation or nest destruction by laying replacement clutches

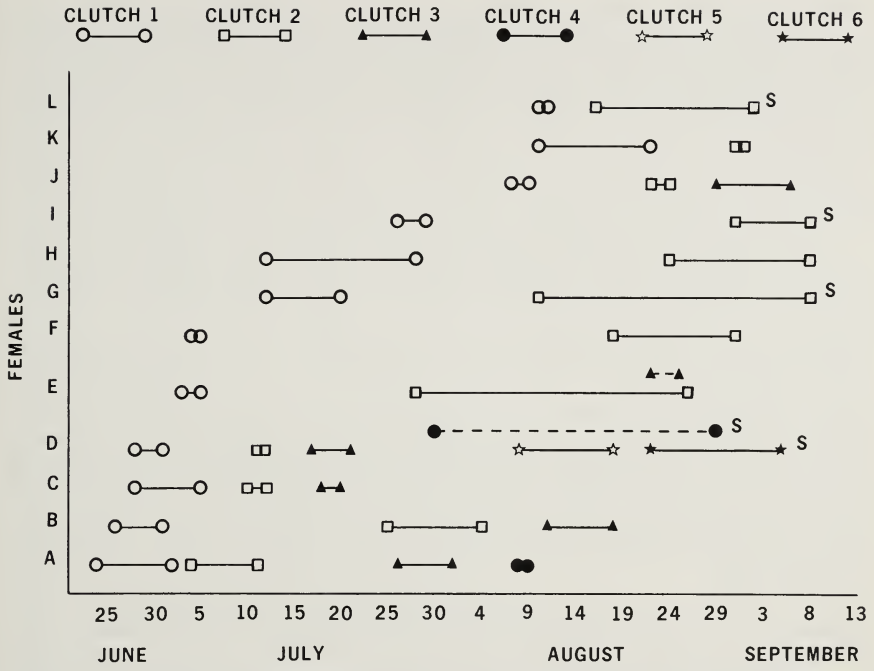


FIG. 1. Nest replacement of marked Wattled Jacanas, 1974 and 1977. Solid line represents clutches of monogamous females; dashed line represents females having pair bonds and mating with another male. S = nests successful in producing at least one young. The length of each line is the duration of each clutch before predation or hatching of young. Data for female A are from Osborne and Bourne (1977).

with the original or different male (Fig. 1). Average interval between the loss of a nest or its contents and the completion of a new nest platform was 10 days (N = 34, range = 2–25).

Females D and E were biandrous (Fig. 1). Female D laid replacement clutches with male WO/O on a small pond from 28 June–21 July. The first nest (one egg), second nest (four eggs) and third nest (four eggs) were trampled by horses. On 30 July she nested with an unmarked male on a small adjacent pond about 20 m distant. This male hatched 3 of the 4 eggs laid. She also held simultaneous pair bonds with male WO/O and actively foraged in and defended each pond. Clutch five incubated by WO/O contained four eggs which were taken by children on 18 August. Clutch six (four eggs), incubated by male WO/O, was successful; one young was seen and both parents gave distraction displays.

Female D laid six clutches of eggs incubated by two different males. With an average weight of 38.7 g/4-egg clutch (Osborne and Bourne 1977), female D potentially laid 232.2 g of eggs (1.37 × her body weight) in 60 days.

Female E and male GW/W mated in a drainage ditch on 3 July. The empty nest was abandoned on 5 July. They remained paired and a second nest was constructed on 29 July. Its four eggs were destroyed on 26 August. While male GW/W incubated this clutch female E held simultaneous pair bonds with male BO/O in the same drainage ditch. The eggs incubated by BO/O were destroyed shortly after the second egg was laid.

Of the 69 nests, 26 (37.7%) were initiated in the wet and 43 (62.3%) during the dry season. Both sexes were reproductively active throughout the study and more nests were successful as breeding progressed. Two of 12 marked females (17%) switched from a monogamous to a polyandrous system. Because females D and E actively defended territories of multiple mates their mating system is classified as a resource defense polyandrous system (Emlen and Oring 1977).

Discussion.—Low success rates of reproductive attempts characteristic of jacanas in this study have also been found in polyandrous Northern Jacanas (Jenni, Am. Zool. 14:129–133, 1974) and Spotted Sandpipers (*Actitis macularia*) (Oring and Knudson, Living Bird 11:59–73, 1972). The ability of females to rapidly lay replacement clutches is also very impressive in phalaropes (Schamel and Tracy, Bird-Banding 48:316, 1977), and in Spotted Sandpipers—in one case a female laid 20 eggs (400% of her body weight) in 42 days (Emlen and Oring 1977).

Both incidences of polyandry and all five successful nests of the marked population occurred during the dry season. Unfortunately we know little about the seasonality of reproduction in Wattled Jacanas. A small marked population was monogamous in the 1974 wet season, but a female was suspected of exhibiting polyandry in August (Osborne and Bourne 1977). Nests have been reported for January, and March–September for Wattled Jacanas breeding in Surinam (Haverschmidt, Birds of Surinam, Oliver and Boyd, Edinburgh, United Kingdom, 1968). In Costa Rica, peak nesting of Northern Jacanas was at the beginning of the wet season but polyandry occurred throughout the year (Jenni and Betts, Anim. Behav. 26:207–218, 1978).

Reproductive success and the occurrence of polyandry may be related to the spatial distribution of resources (Emlen and Oring 1977). Jenni and Collier (1972) found shallow ponds in Costa Rica optimal breeding habitats for polyandrous Northern Jacanas. Interestingly, although ponds and drainage ditches together comprised only 7% of the study area, all successful nestings and polyandrous pairings of the marked population were in these habitats.

Acknowledgments.—I thank C. P. Kennard, A. V. E. Chin and James De Castro for providing housing and logistical support at Burma of MARDS. I am deeply appreciative to Joe De Castro and S. Beissinger for invaluable assistance in the field, and to L. Oring and J. Rising for their constructive reviews of the manuscript. Research in Guyana was funded by grants from the Alumni Foundation of Miami University.—David R. Osborne, *Dept. Zoology, Miami Univ., Oxford, Ohio 45056.* *Accepted 31 Mar. 1981.*

Wilson Bull., 94(2), 1982, pp. 208–212

Habitat of Bachman's Sparrows breeding on Missouri glades.—Bachman's Sparrow (*Aimophila aestivalis*) is an uncommon species occurring locally throughout the southeastern United States. In recent years, declining populations and uncertainty as to the bird's status have led to its being placed on the "early-warning" Blue List (Arbib, Am. Birds, 25–32, 1971–78) and to its designation as "rare" in Missouri by Nordstrom et al. (Rare and Endangered Species of Missouri, Missouri Dept. Conserv. and U.S. Soil Conserv. Serv., 1977). Missouri is at the northwestern border of Bachman's Sparrow breeding range (A.O.U. Check-list Committee, Check-list of North American Birds, 5th ed., Lord Baltimore Press, Baltimore, Maryland, 1957).

Bachman's Sparrows use pine barrens in South Carolina, grassy fields in Mississippi and

tung oil (*Aleurites fordi*) groves in Florida. Many authors have associated Bachman's Sparrows with old-field habitats (reviewed by Hardin and Probasco, Birding, in press).

In 1974 and 1975, Bachman's Sparrows were observed nesting on open limestone glades on the Mark Twain National Forest in Ozark and Taney counties in Missouri. Because previously described habitats do not include glades, we undertook a study in 1976 to determine detailed characteristics of habitats used by Bachman's Sparrows in this plant community.

Glades of the Ozarks are naturally open sites characterized by thin soils usually underlain by limestone. They occur in areas of hilly topography and consist of open grasslands mingled with stands of timber. Approximately 200,000 ha of these glades occur in Missouri.

Methods.—Singing males were located in open glade areas by listening for birds, or by playing a recording and listening for a response. Singing males were observed for 3 h; activities and locations were recorded at 5-min intervals on a map of the area. After at least 10 different locations were recorded for each male, we drew an outline of the territory and calculated the area.

We sampled herbaceous vegetation (grasses, forbs and woody plants less than 1 m tall) within 30 × 65-cm quadrats spaced 5 m apart along transects that crossed the territory at 10-m intervals. Herbaceous cover was estimated for each quadrat and recorded by the Daubenmire ranking method (Daubenmire, Northwest Sci. 33:43–64, 1959).

The territories were marked with a 20 × 20-m grid to sample shrubby vegetation (woody species taller than 1 m and less than 8-cm dbh). At each intersection point, the percent cover was estimated in a circle 4 m in diameter.

We measured trees (greater than 8-cm dbh) using a randomly located 10 × 10-m plot on each territory. Height, crown width and dbh were measured.

Territories.—Twenty-one singing male Bachman's Sparrows were found during 1976 in eastern Ozark and western Taney counties. We mapped 13 territories that ranged in size from 0.3–1.3 ha and averaged 0.62 ha. Nine of the 13 territories had west, northwest or north aspects.

Territories did not have adjoining boundaries. Four territories were found along a slope of one large glade. Distance between nearest edges of territories ranged from 65–100 m. Even in the latter instance, the male in each territory could be heard throughout the adjacent territory. Twice the males on adjacent territories appeared stimulated by one another's song and responded by singing from the closest points of their territories. Only birds in 3 of 13 territories studied were not within human hearing distance of other Bachman's Sparrows.

Nesting.—We found two Bachman's Sparrow nests. Both were located on the ground in 0.25-m-high grassy cover near clumps of little bluestem (*Andropogon scoparius*). Both had been formed by weaving strands of dry grass across the bottom and over the top of grass clumps.

The first nest was found 2 June 1976, when an adult carrying food approached it on the ground from 16 m. The nest at that time contained one partially feathered nestling. The nest was empty on 6 June and neither parents nor young were evident.

The contents of the second nest had been preyed upon when found on 21 June. We suspected the presence of an active nest 19 June because of the excited actions of two adult birds. Parents were not seen 21 June when the nest was discovered some 10 m from its suspected location. One white egg with two small punctures lay on the ground beside the nest.

Evidence of nesting was observed on other territories. A female with grass in her beak was seen 25 May in the presence of a singing male. Young birds were seen on four other territories. The earliest sighting of young was 21 May when two fledglings were seen. Two recently fledged young were seen 15 June on another territory, and on 27 July one fledgling

Table 1

Percent Mean Cover of Grasses and Forbs on 10 Bachman's Sparrow Territories

Vegetation	Territory number											
	1	2	3	4	5	6	7	8	9	10	Average	SD
Little bluestem	43	59	47	47	39	27	43	35	57	52	45	±10
Co-dominant grasses	16	25	15	16	19	16	15	10	14	20	17	± 4
Other grasses	34	22	36	38	53	81	59	63	30	30	44	±18
Composites	18	15	14	8	19	28	30	23	27	21	20	± 7
Legumes	1	1	1	4	1	T	1	T	2	1	1	± 1
Other forbs	10	8	11	11	17	12	12	10	12	10	11	± 2
Total mean cover[a]	122	130	124	124	148	164	160	141	142	134	—	—

[a] Excess of 100% attributable to the layering of vegetational crowns.

was noted on each of two other territories. Of the 21 adult males found, at least 14 had mates. We observed some form of nesting activity in 7 of the 14 mated pairs.

Vegetation.—Herbaceous cover was estimated on 10 of 13 territories mapped (Table 1). Little bluestem dominated the herbaceous vegetation, comprising 40–60% of the cover on all but three of the territories. Cover for co-dominant grasses ranged from 10–25% and cover for other grasses ranged from 22–81%.

Forbs were grouped as composites, legumes and other forbs. Composites formed the dominant forb group. They ranged from 8–30% canopy cover and averaged 20%. Other forbs contributed more to cover than did legumes, ranging from 7–12% of the cover and averaging 11%. The legumes contributed only small amounts to total cover, ranging from a trace to 4% and averaging 1%.

Shrubs and trees made up a small portion of the total cover. Shrub cover occurred on all territories, but only four territories contained any tree cover. Shrub cover for the territories ranged from 0.7–6.8%, averaging 4.1%. Tree cover ranged from 0.9–4.2% and averaged 2.3% over the four territories that had trees.

Eight woody species made up the shrub (less than 8-cm dbh) vegetation. Only two species, fragrant sumac (*Rhus aromatica*) and ash (*Fraxinus* spp.) grew on all territories. Smoke tree (*Cotinus obovatus*) and eastern redcedar (*Juniperus virginiana*) were almost as widespread, being absent from only one or two territories. Only two of the shrub species—smoke tree and eastern redcedar—grew large enough to enter the tree category.

Associated bird species.—Seven other bird species were found in Bachman's Sparrow territories. Of these, Field Sparrows (*Spizella pusilla*) were the most numerous. Prairie Warblers (*Dendroica discolor*) and Brown-headed Cowbirds (*Molothrus ater*) also were seen frequently on the glades, the former feeding and nesting and the latter feeding and parasitizing other birds' nests. Other species with territories overlapping those of Bachman's Sparrow included the Cardinal (*Cardinalis cardinalis*), Blue-gray Gnatcatcher (*Polioptila caerulea*), Mourning Dove (*Zenaida macroura*) and Blue Grosbeak (*Guiraca caerulea*).

Discussion.—Observations of nests, eggs and young verify Bachman's Sparrow as a breeding species on the limestone glades of southwestern Missouri. The presence of 21 singing

males in a relatively small area indicates the bird may be more common than originally thought.

One distinguishing feature characterizing glade habitat is the small amount of woody plant cover above 1 m tall. Kucera and Martin (Ecology 38:285–291, 1957) noted redcedar cover ranged from only a few scattered trees on some glades to a closed canopy on others. More recently, Probasco (pp. 107–109 *in* Proc. Fifth Midwest Prairie Conf., 1976), studying bird use of redcedar cover, reported that Bachman's Sparrows prefer more open cover. Our data corroborate this.

Herbaceous vegetation was dense for all territories, with cover values exceeding 100%, a feature attributable to the layering of vegetational crowns. Comparable herbaceous cover values for areas with moderate and heavy shrub/tree cover were 85% and 45%, respectively (Probasco, unpubl.). Apparently, the birds prefer high density herbaceous cover and low density overstory in the limestone glade region. Typically, this comprises a dense herbaceous stand dominated by grasses and composites with scattered shrubs and trees dominated by fragrant sumac, smoke tree, persimmon (*Diospyros virginiana*), ash and eastern redcedar.

Throughout their range, Bachman's Sparrows use a number of different biotic communities. For example, pine barrens provide important breeding habitat (Weston *in* Bent, U.S. Natl. Mus. Bull. 237, Pt. 2, 1968; Oberholser, The Bird Life of Texas, Univ. Texas Press, Austin, Texas, 1974). Allison (Auk 16:266–270, 1899) found them breeding abundantly in grassy fields in Mississippi and common in pine woods along the Mississippi coastline. In Florida and Georgia, they have adapted to tung oil groves and borders of cultivated fields (Weston *in* Bent 1968). Brooks (Wilson Bull. 50:86–109, 1938) described typical habitat in Ohio and West Virginia as old fields on hilly slopes, with early stages of tree invasion, or open, scattered oak groves in Pennsylvania. Somewhat similar conditions were described by Ridgway (Bull. Nutt. Ornithol. Club 4:218–222, 1879) for Illinois; Gainer (Wilson Bull. 33:3–4, 1921) for Tennessee; and Burleigh (Georgia Birds, Univ. Oklahoma Press, Norman, Oklahoma, 1958) for the Georgia piedmont.

The one unifying feature of most published descriptions of breeding habitat of Bachman's Sparrow is herbaceous cover, usually dense, interspersed with or bordered by some shrubs and trees (reviewed by Hardin, M.S. thesis, Univ. Missouri, Columbia, Missouri, 1977). Maintenance of such conditions can be accomplished by forestry management practices in pine stands of central Louisiana, including a cycle of cutting or thinning and burning that leaves a park-like stand (Meanley, Auk 76:232–234, 1959). In Missouri's glades, prevention of overgrazing and of heavy invasion by eastern redcedar and other woody species seems essential (Hardin 1977).

We found no published information on size of Bachman's Sparrow territories, and thus could not relate territory size to habitat quality. Territories of Bachman's Sparrow in our study (range = 0.3–1.3 ha, $\bar{x}$ = 0.62) were quite similar in size to Field Sparrow territories (range = 0.31–1.62 ha, $\bar{x}$ = 0.76) in an Illinois study in which all available spaces were occupied (Best, Condor 79:192–204, 1977).

In this study, breeding territories of Bachman's Sparrow were not contiguous, and several areas that appeared suitable were not occupied. One possible explanation is competition by the Field Sparrow, a species which appeared to occupy a similar niche and was abundant on the glades. However, no overt signs of competition were witnessed; in fact, Field Sparrows nested and fed within known Bachman's Sparrow territories without apparent strife. These facts, together with the paucity of earlier sightings on the glades, suggest that this may be an expanding population. Bachman's Sparrows may have occupied the glades undetected before the 1950's, but then their numbers were reduced by grazing, drought and repeated burning—all reducing the amount of herbaceous cover. Recent changes in management

practices have begun increasing herbaceous cover. To some extent, then, we may have witnessed repopulation of a formerly depleted habitat.

Acknowledgments.—This study was supported in part by funds from the USDA, Mark Twain National Forest, North Central Forest Experiment Station; and USDI, Missouri Cooperative Wildlife Research Unit, through Cooperative Aid Agreement Number 13–479 with the University of Missouri. We acknowledge contributions by G. E. Probasco to this work.—KIMBERLY I. HARDIN, *School of Forestry, Fisheries and Wildlife, Univ. Missouri, Columbia, Missouri 65211*; THOMAS S. BASKETT, *U.S. Fish and Wildlife Service, Missouri Cooperative Wildlife Research Unit, Univ. Missouri, Columbia, Missouri 65211* AND KEITH E. EVANS, *North Central Forest Experiment Station, Forest Service, USDA, Columbia, Missouri 65211.* *Accepted 10 Mar. 1981.*

Wilson Bull., 94(2), 1982, pp. 212–213

A double-brooded Eastern Kingbird.—Eastern Kingbirds (*Tyrannus tyrannus*) have not been reported to raise more than one brood per breeding season. Apparently, because of the 3–4-week period of post-fledging parental care, the time and energy needed to raise one brood to independence are too great to allow a second brood (Morehouse and Brewer, Auk 85:44–54, 1968). In this note, we report one instance in which a second brood was attempted and discuss reasons for the usual absence of second broods. Our observations were made at the Queen's University Biological Station, near Chaffey's Locks, Ontario, Canada, as part of a study on the factors influencing habitat distribution in the Eastern Kingbird.

For a pair of kingbirds to raise two broods in 1 year they must either lengthen the breeding season by starting earlier of finishing later than usual, thus exposing the adults and young to colder weather and lower insect food levels (see Bryant, Ibis 117:180–216, 1975), or begin the second brood before independence of the first brood, thereby risking lower survival of the first brood. The double-brooded pair we observed appeared to employ the latter alternative.

The first brood consisted of four young until the time of fledging (25 June) when three disappeared. The reason for disappearance was not known but was presumed to be the result of predation since the young had shown normal weight gain as nestlings. The single remaining fledgling, which had been color banded as a nestling, was sighted with the two unmarked adults during four checks of the nest area within the next 2 weeks. The female was found incubating a new clutch of three eggs on 8 July, in a nest located 3 m from the first nest. We calculated clutch initiation date as 4 July by backdating 16 days from hatch (20 July). The 9-day period from fledging to initiation of the second clutch was within the normal time for renesting after failed nests (7.7 ± 1.7 days for 15 pairs). These observations indicated that the same female was responsible for both nests.

During incubation of this second clutch, the adults were observed for three 90-min periods. In the first observation period (14 days after fledging), the fledgling was fed twice by the male and not at all by the female. This feeding rate of 1.3/h is much lower than the usual rate for feeding fledglings which have left the nest in the previous 21 days (6.5 feedings/fledgling/h in our study, 5.6 feedings/fledgling/h calculated from the extensive data in Morehouse and Brewer [1968]). During the other two periods (19 and 23 days after fledging) the fledgling was not fed by either adult despite begging and following behavior. The male vigorously chased

the fledgling from the vicinity of the nest on 10 occasions, a behavior not seen in other parent-fledgling groups. Aggression towards the fledgling stopped after the second nest was preyed upon early in the nestling stage, although parents were not seen to resume feeding of the fledgling (28+ days after fledging). Thus, the reduction in parental care to the fledgling included a low rate of feeding and aggression by the male parent. The response of the male parent could have resulted in injury to the fledgling and at least lowered the amount of protection from predators given to the fledgling.

A female's decision whether or not to start a second brood immediately after the first brood fledges should be governed by the probability of rearing young from the second brood compared to the probability of decreasing the first brood's chances of survival. A comparison of first nests with later renesting attempts for 170 kingbird nests found in 1977, 1979 and 1980 indicated that renests had significantly smaller clutch-sizes (3.13 vs 3.74) and nestling growth rate constants (K of 0.426 vs 0.498, see Ricklefs, Ecology 48:978–983, 1967). In addition, the percent of nests from which young fledged (24.2% vs 54.8%), and the number of young fledged per successful nest (2.25 vs 2.88) were lower for renests vs first attempts. These data indicate that adults have a more difficult time supplying food to their young later in the season and that predation may be higher at this time. Therefore, the advantage gained by attempting a second brood is unlikely to offset the probability of decreased survival for the first brood. It is worth noting that of 68 pairs with successful first broods during 1977, 1979 and 1980, five others fledged only a single young; none of these attempted a second brood.—Peter J. Blancher and Raleigh J. Robertson, *Dept. Biology, Queen's Univ., Kingston, Ontario K7L 3N6, Canada.* *Accepted 13 May 1981.*

Wilson Bull., 94(2), 1982, p. 213

Male Cooper's Hawk breeds in juvenal plumage.—During the summer of 1980 Rosenfield conducted a survey of nesting Cooper's Hawks (*Accipiter cooperi*) in Wisconsin as part of a cooperative study with the Wisconsin Dept. of Natural Resources and the U.S. Fish and Wildlife Service. One objective was to trap and band nesting adults.

On 24 June 1980, while attempting to trap breeding adult Cooper's Hawks in southwestern Dane County, a male in juvenal plumage flew to the nest carrying prey. It dropped the food and flew off, but subsequently returned and was caught. The yearling's eye was a light orange; only five primaries and two rectrices were of adult plumage. The female (not caught) was in adult plumage. There were five young, about 1 week old, in the nest. The nest was deserted by 11 July. We found the remains of two young near the base of the nest tree. The cause of nesting failure was unknown.

Rosenfield observed 20 breeding Cooper's Hawks (12 females, 8 males) at 14 nests; only the above-mentioned male was in juvenal plumage. Meng (Ph.D. diss., Cornell Univ., 1951:47) reported 2 of 36 and Reynolds and Wight (Wilson Bull. 90:192, 1978) reported 2 of 34 Cooper's Hawk pairs with females in immature plumage, but reported no known nesting immature males. Kline (J. California Hawking Club 5:17, 1975) reported a nesting male Cooper's Hawk in juvenal plumage, paired with a juvenile female, in California. His account and this note are, to the best of our knowledge, the only records of such an occurrence.

We would like to thank R. Anderson and W. Smith for their support of this study and F. and F. Hamerstrom, and H. Mueller for reviewing this note.—Robert N. Rosenfield, *College of Natural Resources, Univ. Wisconsin-Stevens Point, Stevens Point, Wisconsin 54481* and Jonathan Wilde, *Rte. 1, Box 69, Belleville, Wisconsin 53508.* *Accepted 15 June 1981.*

Wilson Bull., 94(2), 1982, p. 214

Unusual feeding behavior by a population of Black Vultures.—Vultures are usually characterized as carrion feeders. Black Vultures (*Coragyps atratus*) are often referred to by the vernacular name "carrion crow" (Townsend, U.S. Natl. Mus. Bull. 167, 1937). There are, however, numerous reports in the literature indicating that it is not unusual for vultures to use other foods, including vegetable matter. For example, the Vulturine Fish Eagle or Palm Nut Vulture (*Gypohierax angolensis*) is primarily vegetarian, subsisting mainly on oil palm (*Elaeis guineensis*) fruits (Brown and Amadon, Eagles, Hawks and Falcons of the World, 1968; Brown, African Birds of Prey, 1971). Crafts (Wilson Bull. 80(3):327–328, 1968) observed Turkey Vultures (*Cathartes aura*) feeding on coconut and Green (Bird-Lore 29:117–118, 1927) reported this species eating pumpkin. Haverschmidt (Condor 49(5):210, 1947; Birds of Surinam, 1968) mentions that Black Vultures feed on oil palm fruits and copra in addition to offal.

However, except in the case of the Vulturine Fish Eagle, each of these reports implied that vegetable matter is incidental to the normal carrion diet. Both Crafts (1968) and Green (1927) emphasized that vegetable matter was not a preferred food and was probably taken only because of a lack of carrion. We have observed an instance in which a population of Black Vultures may have developed a preference for vegetable matter over carrion.

The plantation "La Arenosa" is located near the town of Turbo in northwestern Colombia. About half of the 200 ha-plantation is devoted to African oil palm. Vultures were feeding on harvested oil palm fruits to a degree sufficient to alarm the plantation operators. Racemes of fruit are harvested from the palms throughout the year, and piled on platforms at various points along roadways throughout the plantation. They remain there for a short time (up to a day) awaiting transport to the oil extraction plant. Vultures congregate at these platforms in groups of 10–50 and feed on the small (4 cm) fruits, generally removing the soft husk and discarding the nuts. Though we observed some birds feeding in the trees, this behavior was not common; most feeding was at the platforms, primarily during the morning and evening hours, and according to the plantation manager, occurred year-round. Vultures are protected by law in Colombia, hence we did not attempt to collect any. We did examine 10 birds killed and brought to us by workers (presumably on orders of the manager). We visually estimated the crop content to be 95% or more oil palm fruit and the remainder unidentified material. On the basis of the estimated number of birds in the population (about 500) and the weight of fruit in the crops, we calculated a potential daily loss of $150–200 (U.S.), a substantial loss over a year's time. Although the sample was probably biased (i.e., birds killed while feeding on the palm fruit), this does not detract from the significance of the economic impact.

Carrion was not readily available on the plantation, and among various remedies tried was deliberate placement of four livestock carcasses on the plantation. These were left in place for over a week. During this time they were completely ignored by the vultures who continued feeding on oil palm racemes. This, plus the fact that carrion was available on lands surrounding the plantation, suggests that the vultures may have developed a preference for the oil palm fruit. The Vulturine Fish Eagle reportedly will reject meat in favor of oil palm husk. Oil palm fruit is rich in carotene (a precursor of Vitamin A) but the suggestion that the need for this vitamin is the basis for the food preference of the fish eagle is unfounded; apparently oil palm nuts are a favorite food (Brown and Amadon 1968). Oil palm is a relatively recent crop in this area of Colombia and it may be that Black Vultures simply prefer it to carrion when they have a choice.

Support for this work was provided by the U.S. Agency for International Development, the Instituto Colombiano Agropecuario and the La Arenosa Oil Palm Plantation.—Donald J. Elias, *Denver Wildlife Research Center, Denver, Colorado 80225* and Danilo Valencia G., *Instituto Colombiano Agropecuario, Palmira, Colombia.* *Accepted 15 Apr. 1981.*

Wilson Bull., 94(2), 1982, p. 215

Clapper Rail preys on Savannah Sparrow.—At 14:00 on 24 April 1980, while conducting field studies at the Tijuana Salt Marsh, California (N32°30′, W117°07′), we heard high pitched calls coming repeatedly from a small clump of cordgrass (*Spartina foliosa*) about 30 m away. We then saw an adult Clapper Rail (*Rallus longirostris levipes*) running along the edge of the cordgrass being pursued and attacked by two scolding Savannah Sparrows (*Passerculus sandwichensis beldingi*). The rail was carrying a small bird in its bill. The rail then ran back into the cordgrass cover, but upon our closer approach flushed without its prey. At the site from which the rail flushed, we found an adult Savannah Sparrow lying motionless but still alive. It had fresh puncture wounds in its rump and sides. Age of the sparrow was based on the presence of a full set of worn primary feathers and bright yellow lores. We replaced the injured sparrow and returned to our original vantage point for 15 min; the rail did not return to its prey.

Interaction between this rail and this sparrow is not surprising since their range and habitat widely overlap in coastal California (Wilbur, Am. Birds 33:251, 1979; Massey, Belding's Savannah Sparrow, S. California Ocean Stud. Consort. of the Calif. State Univ. and Colleges, 1979).

Clapper Rails have a diverse diet composed mainly of live invertebrates and small fish found in marshes. Oney (J. Wildl. Manage. 15:106–107, 1951) and Martin et al. (A Guide to Wildlife Food Habits, McGraw-Hill, New York, New York, 1951) reported crabs, molluscs, insects, snails, fish, worms and various marsh plants found in Clapper Rails collected on the East Coast. On the west coast, Moffit (Condor 43:270–273, 1941) reported that crayfish were the principle foods of 32 Clapper Rails taken along the Colorado River and in Mexico. However, in addition to other food items they also reported the presence of feathers in two of their samples. A Clapper Rail attacked a Gray Catbird (*Dumetella carolinensis*) in a mist net in New Jersey (Spendelow and Jeffrey, J. Field Ornith. 51(2):175–176, 1980). It is not clear whether the Clapper Rail was taking the mist-netted birds for food or whether this was a territorial response. Meanley (King Rail, N. Am. Fauna No. 67, 1969) also found some feathers in stomach samples from the closely related King Rail (*Rallus elegans*), along with vertebrae of a female Red-winged Blackbird (*Agelaius phoeniceus*). Aside from these reports, the extent of Clapper Rail interaction with other bird species, particularly as predator, is still poorly documented.—Paul D. Jorgensen and Howard L. Ferguson, *Code 1843, Natural Resources, Bldg. 3, Naval Air Station North Island, San Diego, California 92135.* *Accepted 15 June 1981.*

Wilson Bull., 94(2), 1982, pp. 215–216

Commensal feeding of Little Blue Herons with manatees.—Symbiotic feeding of egrets and herons with large terrestrial vertebrates is well known (see review by Kushlan, Natl. Audubon Soc. Res. Rept. No. 7, 1978a). Kushlan (Auk 95:677–681, 1978b) has also observed Little Blue Herons (*Hydranassa caerulea*) feeding commensally with White Ibis (*Eudocimus albus*) and has suggested that many associations of water birds may also be commensal. This report describes the behavior of one or more Little Blue Herons associating with manatees (*Trichechus manatus*) in the St. Johns River near DeLand, Volusia Co., Florida.

On 23 January 1978, a Little Blue Heron was observed on a raft of water hyacinth (*Eichhornia crassipes*) while a manatee was feeding on the hyacinth nearby. The manatee surfaced 21 times over 19 min before leaving the area. Each time the manatee created a disturbance

in the vegetation the heron immediately moved toward the manatee. The heron peered at openings created in the vegetation by the manatee, and made several feeding strikes. It could not be determined how many strikes were made or if any were successful.

On 13 February 1978, similar behavior was seen on another hyacinth raft 400 m from the original observation site. On this occasion, a Little Blue Heron was noted catching small fish at manatee-created openings by hopping and striking, or by using the stand-and-wait method described by Meyerriecks (Nutt. Ornithol. Club No. 2, 1960). The heron made 27 strikes, 21 of which were successful (78%) during 48 min. By contrast, another Little Blue Heron, not associated with a manatee, was observed at the same time on a hyacinth raft 100 m away using only the stand-and-wait method. It made 16 strikes within 45 min, 7 of which were successful (44%). A Little Blue Heron was briefly observed investigating manatee-created disturbances in the same area on 14 and 17 February 1978, but on both occasions the manatee departed after 5 min and no feeding strikes by the heron were seen.

Feeding in association with manatees may have increased the heron's feeding success. The disturbance caused by the manatee surfacing and grasping plants may have flushed out fish or invertebrates associated with the hyacinths. Kushlan (1978b) reported that Little Blue Herons in commensal association with White Ibis preyed on small fish flushed by the movements of the ibis. Strike rates were higher for herons feeding commensally with ibis than for herons feeding alone, but strike success rate was the same in both situations, suggesting that prey was more available, but not more vulnerable to the commensally associating herons.

While manatees are not abundant in Florida, a number frequently feed at these hyacinth rafts on the St. Johns River and thus present a localized opportunity for commensal feeding by the herons, particularly since Little Blue Herons are noted for specialized and opportunistic feeding behaviors (Kushlan, 1978a).

Acknowledgments.—We are grateful to B. Irvine, F. Sorrenson and J. Waldron for assistance during field observations. B. Irvine, R. Banks, G. Rathbun and A. Meyerriecks made constructive comments on the manuscript.—MICHAEL D. SCOTT AND JAMES A. POWELL, *National Fish and Wildlife Laboratory, Gainesville Field Station, 412 N.E. 16th Avenue, Gainesville, Florida 32601.* (Present address MDS: *Inter-American Tropical Tuna Commission, % Scripps Institution of Oceanography, La Jolla, California 92037.*) *Accepted 10 Aug. 1981.*

Wilson Bull., 94(2), 1982, pp. 216–218

Comparison of the nest-site distraction displays of Black-capped Chickadee and White-breasted Nuthatch.—It is the purpose of this paper to describe an unusual distraction display at the nest-site by the Black-capped Chickadee (*Parus atricapillus*) and to compare it to the very similar display of the White-breasted Nuthatch (*Sitta carolinensis*). Observations reveal that these nest-site distraction displays are neither "injury feigning" (formerly ascribed to chickadees) nor "death feigning" (apparently a lapsus, ascribed to or at least implied for nuthatches). Works on other parids and sittids were reviewed to learn the general characteristics of nest-site distraction displays reported in these closely related families. Verification, re-description and some undescribed aspects of the nest-site displays of both chickadees and nuthatches are reported.

Observations were made on nesting nuthatches over a five-year period (1976–1980). All the distraction displays were made to red (*Tamiasciurus hudsonicus*) and gray (*Sciurus carolinensis*) squirrels and eastern chipmunks (*Tamias striatus*). All observed displays (with one possible exception) occurred within 2 m of a nest cavity situated about 5 m above ground in a red oak (*Quercus rubra*) outside my window, in Stevens Point, Portage Co., Wisconsin.

The cavity was first used by the nuthatches, but in the fall of 1979 a family of six young red squirrels were reared in the cavity, and after they departed a pregnant gray squirrel found winter shelter inside. That same squirrel reared its young (seen 28 May 1980) in a leaf nest nearby, and occasionally encountered the nesting pair of nuthatches. The opening of the nest hole was about 4–5 cm across. Nesting chickadees (one clutch and brood) were observed in the spring of 1980, at a nest box set 1.5 m above the ground.

Distraction displays were induced by a young, live fox snake (*Elaphe vulpina*) and stuffed skins of gray squirrel, red squirrel, least chipmunk (*Eutamias minimus*), southern flying squirrel (*Glaucomys volans*), long-tailed weasel (*Mustela frenata*) and white-footed mouse (*Peromyscus leucopus*). To induce a distraction display the snake or mammal was hoisted up along the tree trunk toward the nesting site by means of nylon fishing line and a simple screw-eye placed above tne nest cavity. Ordinarily I did not hide myself; the stuffed mammal induced the distraction displays so long as I was at a distance from the nest.

Having observed often the nest-site distraction display in the White-breasted Nuthatch I was struck by its close resemblance to a nest-site display (26 May 1980) by Black-capped Chickadees (the body horizontal, perched on a branch) made to a House Wren (*Troglodytes aedon*) and subsequently to an eastern chipmunk (18:30). The latter display was full, meaning that the wings were fully extended.

The nest-site display by the parent chickadees was induced six times by using a stuffed red squirrel, gray squirrel and white-footed mouse (four times). The display was a threat, often preceding or following aerial attacks by the parents. For example, both parents flew at the stuffed gray squirrel until it fell to the ground. One chickadee flew down to a branch about 1.5 m above the ground and presented the squirrel a full display. The bird leaned forward with wings extended until it slightly lost its balance, and one wing fell against a leaf. The chickadee moved its head from side-to-side displaying the white auricular patches. White feathers were evident in the widely flared tail.

Occasionally, a bird displayed alone, but sometimes both sexes displayed. Exactly as in nuthatches, the wings were more or less extended, the bird usually faced the predator, swaying from side-to-side, twisting its body right and left, the head held forward and downward and the tail flared.

The chickadees displayed even to a live snake placed above the nest box. The female observed the snake, flitting close (0.3 m) to it, the chickadee's body swaying, head moving from side-to-side. There was no sound. The male arrived, sounded a *chick-a-dee-dee*, hovered near the snake, and repeatedly struck it with his bill, driving it away. The female then flew to a nearby pine (*Pinus* sp.) branch (2 m away) and gave a full distraction display, including the wing flutter. This display was not seen by the snake. By lifting the snake toward the female, I drove her from tree-to-tree and induced two more displays. The chickadees did not display to me while I handled the young, but one partially displayed to my 11-year-old son.

When attacking in flight the chickadees usually gave a cry—*fzzz* (probably the *zee* call made to several predators reported by Ficken and Witkin [Auk 94:156–157, 1977] who observed "no noticeable alarm reaction" of any kind toward either red or gray squirrels by birds at feeders). Prior to a full display to the red squirrel one parent bringing food flew to a nearby branch, pecked at and finally ate the larval insect.

Other reports on distraction displays in parids are few, brief and often misleading. Grimes (Auk 53:478–480, 1936) briefly mentioned "injury feigning" in the "Florida Chickadee" (*P. carolinensis*). Pettingill (Bird-Lore 39:277–282, 1937) described a distraction display on Grand Manon in the "Acadian Chickadee" (*P. hudsonicus*). This bird, displaying in the proximity of a red squirrel, spread its wings full, but fell over backward from its perch. The Black-capped Chickadee usually leans forward to display. Odum (Auk 58:314–333, 518–535, 1941;

59:499–531, 1942) considered the display in the Black-capped Chickadee as "injury feigning," and described it fairly well: ". . .wings were held outstretched and slowly flapped back and forth over the back, the head held straight out and moved slowly from side to side in a grotesque motion." Odum (1941) mentioned that squeaking by the young was necessary to evoke the display behavior, but my observations proved otherwise.

Hinde (The behavior of the Great Tit (*Parus major*) and some other related species. Behaviour, Suppl. II, 1952) reported a display made in winter to a gray squirrel within its drey by a Great Tit (*P. major*). The display was then repeated at the drey three more times. No such display was ever seen again, even when a squirrel approached a nest with fledglings leaving it. Hinde (1952) also quoted a report by Butler in which a palm squirrel (*Funambulus palmarum*) was "mobbed" at a nest by a female *Machlolophus haplonotus*, "with wings spread and feathers erect." I have found no reports of nest-site distraction displays in sittids other than those of the White-breasted Nuthatch.

In my study, the White-breasted Nuthatch's nest-site display was observed on 11 occasions. The display was also induced, 40 times, by hoisting stuffed mammals and a fox snake near the nesthole. The male made displays more often than did the female, and moved about much more actively to different positions to threaten the predator. The female usually stayed nearer the nest. The male twice moved down to the base of the tree trunk to display to a stuffed mouse.

Displays were made as follows: to a stuffed red squirrel (four full, eight partial), flying squirrel (four full, five partial), gray squirrel (three full, one partial), least chipmunk (four full), long-tailed weasel (one full, two partial), white-footed mouse (five full), fox snake (one full, one partial) and an 8-inch (203 mm) stick (none). Previously, nuthatches were known to display only to red and gray squirrels, eastern chipmunks and possibly to other birds (Teale, Audubon 76(6):50–53, 1974). The most display sites on the nest tree used to threaten a predator were five (one of these by the female near the hole).

Generally, only the male called during displays. However, often he did not, especially not for the snake and the mouse. Sometimes he did not call for as long as 10 min, then called incessantly. The call was usually *waawaawaawa*, a call comprised of 4–5 syllables. Once the call was in paired syllables, with an occasional *tutu*.

The similar size, grayish color, black cap and white auricular patches make the unusual and aggressive nest-site distraction displays of these two birds all the more similar. In both species the display is a bold threat to potential nest robbers, especially small mammals such as squirrels. Differing from the nuthatch display (see Stoner, Auk 60:95–96, 1943; Kilham, Auk 85:477–492, 1968) is the flutter of the wing by the chickadee, which seems an attempt to regain balance, but in fact, is usually a component of the display. Furthermore, the chickadee often flies forward to peck at the predator striking it with surprising force. The nuthatch is more likely to make the display while hanging by the feet from a branch or the bark of a vertical tree trunk, whereas the chickadee usually perches on branches. Many display poses of the nuthatch are therefore peculiar. Kilham's (1968) description of the display is excellent, but one may assume (as did Skutch, p. 143 *in* Parent Birds and Their Young, Univ. Texas Press, Austin, Texas, 1976) that the display is usually made in an upright position. In my observations most displays were made head downward, as in the chickadee display. The nuthatch generally faces the predator and as a last resort will peck its nose. In both the chickadee and nuthatch the display is occasionally made so far away from the predator that probably it goes unnoticed. Generally the white wing spots (set off by black) are prominently displayed by the nuthatch, but these are lacking in the chickadee.

I thank Professor Richard F. Johnston of the University of Kansas Museum of Natural History for his criticisms of the manuscript.—CHARLES A. LONG, *Museum of Natural History and Dept. Biology, Univ. Wisconsin, Stevens Point, Wisconsin 54481.* *Accepted 12 Mar. 1981.*

Wilson Bull., 94(2), 1982, pp. 219–223

A review of hybridization between *Sialia sialis* and *S. currucoides*.—Hybridization between Eastern Bluebirds (*S. sialis*) and Mountain Bluebirds (*S. currucoides*) in Manitoba was first reported by Lane (Auk 85:684, 1968). Lane identified, observed and collected a hybrid male that had backcrossed polygynously with females of both species. The Eastern Bluebird female produced infertile eggs, but the Mountain Bluebird female laid two viable clutches. Lane suggested that hybrids were fertile only with *S. currucoides*.

Since the first record in 1967, 19 additional cross-breedings have been reported in Manitoba and one in Saskatchewan. Most have been reported anecdotally or incompletely in regional journals, but neither complete accounts nor a summary is available. Herein we review the existing records.

The 21 records include every combination of *S. sialis*, *S. currucoides* and hybrid except *S. sialis* male × hybrid and hybrid × hybrid (Table 1). Data show that hybrid males backcrossed equally to females of both species, but female hybrids have been observed backcrossed only to Mountain Bluebird males.

Mean clutch-size was 5.25±0.87 eggs for the 16 nests in which numbers of eggs were known. Clutch-size varied little among breeding pair combinations, as follows: hybrid male × *S. sialis* female: $\bar{x}$ = 5.0 (N = 3); hybrid male × *S. currucoides* female: $\bar{x}$ = 5.7 (N = 3); *S. currucoides* male × hybrid female: $\bar{x}$ = 5.25 (N = 4); *S. sialis* male × *S. currucoides* female: $\bar{x}$ = 5.5 (N = 2); *S. currucoides* male × *S. sialis* female: $\bar{x}$ = 5.0 (N = 3). Average clutch-sizes are generally smaller than the $\bar{x}$ of 5.7 ± 0.58 eggs recorded for 139 nests of Mountain Bluebirds in southwestern Manitoba (Munro et al., Auk 98:181–182, 1981), but larger than those of Eastern Bluebirds in Manitoba ($\bar{x}$ = 4.69 ± 0.79, N = 16) (Rounds and Munro, unpubl.) and the eastern United States (Laskey, Bird-Banding 10:23–32, 1939; Peakall, Living Bird 9:239–255, 1970).

A hatching rate of 87% occurred in all nests with known numbers of eggs (Table 2). Fertility was high (94–100%) in all breeding pair combinations except hybrid males × Eastern Bluebird females, where only 5 of 15 eggs hatched in three separate nests. Reported hatching rate for undisturbed nests of Eastern Bluebirds was 92–98% (Peakall 1970). Fertility and hatching in cross-breeding pairs, therefore, compares favorably with normal pair performance.

All nests involving mixed pairs were located in southwestern Manitoba, except one near Saskatoon, Saskatchewan (Table 2, Fig. 1). The incidence of nests near Brandon doubtless reflects the density of nest boxes there, and the concentration of cross-breeding pairs in southwestern Manitoba coincides with the area of maximum overlap in the breeding ranges of the two species (Zeleny, The Bluebird, Indiana Univ. Press, Bloomington, Indiana, 1976). The Eastern Bluebird is apparently extending its range westward into Saskatchewan (Scott, Blue Jay 24:186–187, 1966; Ashdown, Blue Jay 24:187, 1966; Belcher, Blue Jay 24:187–189, 1966) and Alberta (Butot, Blue Jay 36:41, 1978).

Records of the number of nest boxes checked, bluebird pairs observed and cross-breeding pairs reveal considerable variation in population ratios between the two parent species (Table 1). As the number of nest boxes increased through time, the initially low populations of *S. sialis* and *S. currucoides* increased rapidly. Populations of Mountain Bluebirds, however, increased more rapidly than those of Eastern Bluebirds and early interspecific ratios near unity became heavily skewed toward Mountain Bluebirds. A significant decline in numbers of Eastern Bluebirds began in 1975, and recovery has not occurred. Mountain Bluebirds have remained plentiful, and, when data are adjusted to account for differences in number of nest boxes monitored, populations continue to increase.

Table 1

Ratio of *S. sialis* to *S. currucoides* and the Incidence of Cross-breeding and Hybrid Backcrossing in Manitoba

Year	No. boxes monitored	No. first-brood nests			Hybridizing pairs	
		S. currucoides	*S. sialis*	Ratio *S.c./S.s.*	N	% nests
1963	749	28	22	1.27	0	0
1964	740	50	29	1.72	0	0
1965	774	66	40	1.65	0	0
1966	801	79	47	1.68	0	0
1967	1200	160	55	2.91	1	0.47
1968	1400	242	60	4.03	0	0
1969	2100	350	65	5.38	0	0
1970	2400	435	113	3.85	2	0.37
1971	3000	508	135	3.76	3	0.46
1972	3500	715	175	4.09	5	0.56
1973	4100	825	150	5.50	1	0.10
1974	4355	950	160	5.94	3	0.27
1975	789	333	9	37.00	1	0.29
1976	1109	410	38	10.79	2	0.45
1977	941	405	33	12.27	0	0
1978	1092	552	10	55.20	0	0
1979	1000	473	27	17.52	0	0
1980	1059	334	12	27.83	1	0.29
Totals	31,109	6915	1180	5.86	19	0.24

Cross-breeding and hybrid backcrossing were not found in 9 of 18 years for which we have data. Mixed pairs account for 0.10–0.56% of all breeding pairs in those years when interbreeding occurred, suggesting that hybridizing is rare. Ten of the 18 pairings occurred between 1970 and 1974, when high populations of both species were present. The 18-year average ratio between parent species was approximately 6:1 in favor of *S. currucoides*, and the rate of mixed species pairings was 0.24% for 8114 pairs.

Only the original hybrid male has been described in detail (Lane 1968). This bird had mixed blue and red feathers on the breast, but had the blue back, wings and tail, and voice of *S. sialis*, and resembled *S. currucoides* in general behavior. The hybrid was intermediate in size between the two species. Lane's field notes indicate that all subsequent hybrid males were similar to the first in plumage.

Spear (Blue Jay 33:231, 1975) reported a hybrid female with rusty-brown feathers scattered throughout the grey breast. Spear (pers. comm.) indicated that all three hybrid females that he had seen were similar in general appearance and resembled female *S. currucoides* more than female *S. sialis*.

The 1980 hybrid female differed from those reported by Spear (1975) in that it resembled a Mountain Bluebird female with dull chestnut breast and flanks and a deeper blue on the back. In-hand the bird was seen to lack blue or grey in the head, neck and upper back, and to have no throat patch. The three juveniles from her first brood all had chestnut in the breast and flanks following the first plumage change. The five young of the second brood

Table 2

Characteristics and Locations of 21 Cross-bred or Hybrid Backcrossed Pairs of *Sialia* in Canada

Year	Pair: male	Pair: × female	No. eggs	No. young	Location[a]	Reference
1967	Hybrid [b]	× *S. currucoides*	7	6	Oak Lake	Lane 1968
	Hybrid]	× *S. sialis*	5	0	Oak Lake	Lane 1968
1970	*S. sialis*	× *S. currucoides*	—	4	Carberry	Lane and Knock, Blue Jay 29:209, 1971
	S. sialis	× *S. currucoides*	6	6	Kenton	Lane and Knock 1971
1971	*S. currucoides*	× *S. sialis*	—	4	Kemnay	Lane and Knock 1971
	S. sialis	× *S. currucoides*	—	3	Kenton	Lane and Knock 1971
	Hybrid	× *S. sialis*	6	1	Routledge	Lane and Knock 1971
1972	*S. sialis*	× *S. currucoides*	6	6	Glenboro	Lane and Bauman, Blue Jay 30:226–227, 1972
	Hybrid	× *S. currucoides*	5	5	Carberry	Lane and Bauman 1972
	S. sialis	× *S. currucoides*	—	3	Griswold	Lane and Bauman 1972
	Hybrid	× *S. currucoides*	5	5	Griswold	Lane and Bauman 1972
	S. sialis	× *S. currucoides*	5	5	Griswold	Lane and Bauman 1972
1973	Hybrid	× *S. sialis*	4	4	Shilo	Lane and Martin, Blue Jay 31:235–236, 1973
1974	*S. currucoides*	× *S. sialis*	—	2	Grande-Clairiere	Lane and Burton, Blue Jay 32:238–239, 1974
	S. currucoides	× *S. sialis*	4	4	Sidney	Lane and Burton 1974
	S. sialis	× *S. currucoides*	—	4	Shilo	Lane and Burton 1974
	S. currucoides	× *S. sialis*	5	5	Saskatoon, Sask.	Houston, Blue Jay 32:240–241, 1974
1975	*S. currucoides*	× *S. sialis*	6	6	Russell	Lane and Black, Blue Jay 33:243–245, 1975
1976	*S. currucoides*	× Hybrid	6–5–3[c]	6–5–[d]unk.	Russell	Lane et al., Blue Jay 34:208–209, 1976
	S. currucoides	× Hybrid	5	5	Russell	Lane et al. 1976
1980	*S. currucoides*	× Hybrid	unk.–5[e]	3–5[d]	Lyleton	New record

[a] All locations are in Manitoba, with the single noted exception.
[b] Polygynous male.
[c] First, second and third clutches.
[d] First and second broods.
[e] First and second clutches.

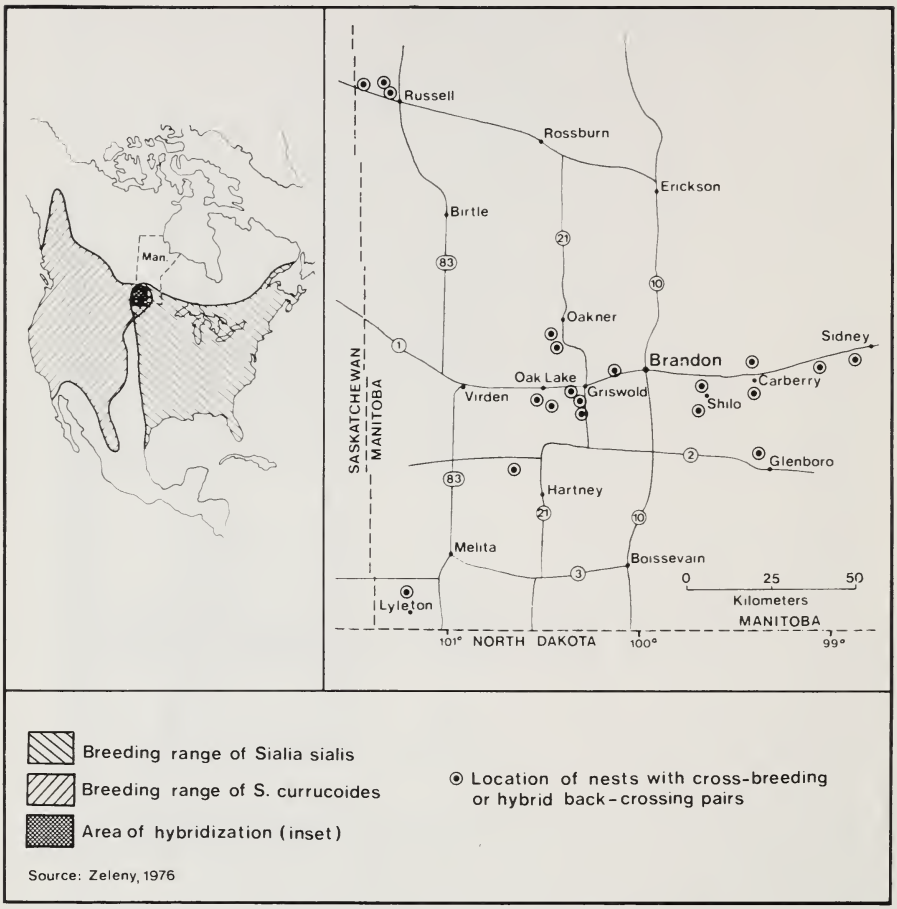


FIG. 1. Breeding ranges and the location of cross-breeding and hybrid backcrossing pairs of *Sialia* in North America.

resembled *S. currucoides* juveniles, without obvious intermediate plumage. We observed the fledging of the second brood and the adults were assisted in feeding the fledglings by the first brood.

Characteristics of the hybrids are clearly combinations of the two parent species, and a gradual geographic transition in characters from one form to another is not evident. In the absence of evidence of dominance in cross-breeding or introgression, we see no grounds to combine *S. currucoides* and *S. sialis* as a single species. The confinement of hybridization to the small area where breeding ranges overlap is not uncommon in birds, and the rarity of hybridization within this zone suggests that genetic exchanges are minimal between the parent populations.

We thank Norah Lane, James Spear, Earl Howden and John Murray for assistance in collating information. The 1980 field research was funded by a Research Award to Munro

from the Natural Sciences and Engineering Research Council, Canada, and Brandon University.—Richard C. Rounds and Hugh L. Munro, *Dept. Geography, Brandon Univ., Brandon, Manitoba, R7A 6A9 Canada.* *Accepted 5 Mar. 1981.*

Wilson Bull., 94(2), 1982, p. 223

Interspecific plumage similarity: the Mockingbird and Loggerhead Shrike.—Interspecific deception may be widespread in animals. For example, avian vocal mimics often produce sounds similar to those of large, aggressive or predatory species, and such mimicry might dissuade rivals from living in that locality by making it appear to be inhabited by predators and/or competitors (Rechten, Anim. Behav. 26:305–306, 1978). We suggest that the Mockingbird (*Mimus polyglottos*) exhibits plumage similarity with a predator, the Loggerhead Shrike (*Lanius ludovicianus*). The Mockingbird looks very much like a shrike, the two species being of similar size, although the shrike is somewhat chunkier. Even Robbins' bird guide states that the shrike is "often confused with the mockingbird" (Robbins et al., Birds of North America, Golden Press, New York, New York, 1966). Plumage similarities include gray back, lighter breast, white patches on the wings and dark gray tail edged with white. The chief differences are more subtle: the shrike has a black line through the eye and a hooked bill. Both commonly use elevated perches in open habitat. Hailman (Wilson Bull. 72:106–107, 1960) observed Barn Swallows (*Hirundo rustica*) mobbing a Mockingbird and suggested that the swallows mistook the Mockingbird for a shrike.

The similarity between these two species might be considered a case of mimicry in which selection favored Mockingbirds that looked like the predaceous shrike. Almost complete range overlap occurs for the two species. However, outside the shrike's range other mockingbird species occur that are very similar in plumage to *M. polyglottos*, e.g., Tropical Mockingbird (*M. gilvus*), Patagonian Mockingbird (*M. patagonica*) and White-banded Mockingbird (*M. triurus*). Therefore, we think that the similarity between *M. polyglottos* and *L. ludovicianus* is not a result of selection for plumage resemblance.

The Mockingbird is well known for its pugnacity in defending year-round territories (Bent, U.S. Natl. Mus. Bull. 1948). Apparently, Mockingbirds face intense interspecific competition in winter with other frugivores and sometimes respond aggressively to them (Moore, Behav. Ecol. Sociobiol. 3:173–176, 1978). No studies have investigated interspecific competition during the breeding season. We hypothesize that despite the origins of plumage similarity of Loggerhead Shrikes and Mockingbirds, the Mockingbird may benefit from the similarity because other species are sometimes deceived by the resemblance, reducing the probability of their remaining in an area so populated with "predators." Perhaps other cases of resemblance that have been considered mimicry may simply be the outcome of convergent evolution.

We thank K. Apel and R. Balda for their comments. Contribution No. 30 of the University of Wisconsin-Milwaukee Field Station.—Robert W. Ficken and Millicent S. Ficken, *Dept. Zoology, Univ. Wisconsin–Milwaukee, Milwaukee, Wisconsin 53201.* *Accepted 3 Sept. 1981.*

Wilson Bull., 94(2), 1982, pp. 223–225

Head wind promotes skimming in Laughing Gulls.—The evolutionary origin of skimming behavior in skimmers (Rynchopidae) such as the Black Skimmer (*Rynchops niger*) is uncertain. Observations of the occurrence and conditions promoting similar behavior in

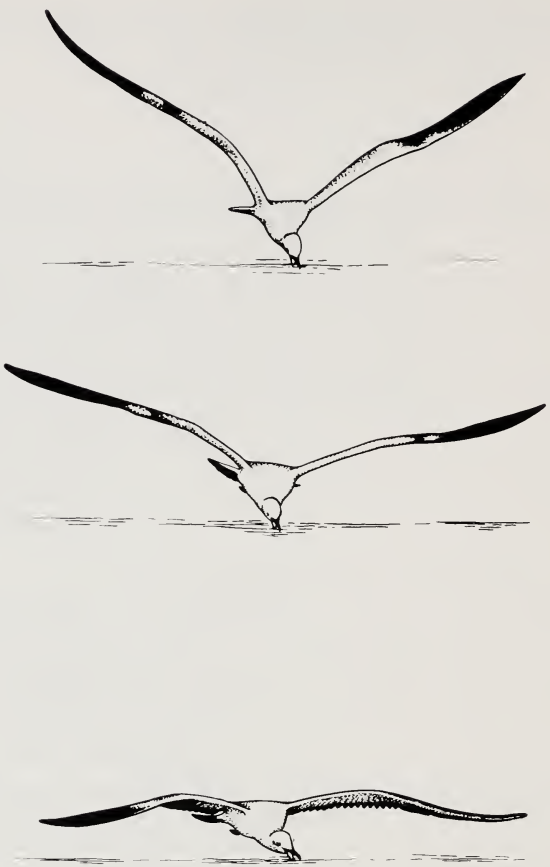


FIG. 1. Wing positions of skimming Laughing Gulls drawn by Cheryle Hughes from photographs by J.P.H. The first two examples are from a skimming sequence of a single bird; the third is from another sequence and may represent a different individual.

other larid species are therefore useful clues to the origin of skimming. Here we report the first observations of skimming in the Laughing Gull (*Larus atricilla*) and the wind conditions that promoted it.

We observed approximately 40 skimming bouts in a minimum of six gulls in breeding plumage and four in winter plumage on 24 March 1980, at Eco Pond, 100 m north of the campground at Flamingo in Everglades National Park, Dade Co., Florida. From 08:45–10:15 EST we watched gulls flying at a height of 3–5 m descend to the water's surface and insert the distal one-third of their lower mandibles into the water one to several times, each time cutting a wake of 0.3–2 m. Frequently the bird suddenly depressed its tail or lowered its feet upon approach to the water, presumably to break its thrust. Thereupon it would fly slowly over the water with shallow wingbeats or glide parallel to the water's surface and skim. Our telephoto pictures show that the wing position varies from horizontal (with a noticeable bow

upward at the carpal joint) to a raised angle of about 40° with respect to the water (Fig. 1). The distance between bill immersions within a bout varied from about 2–20 m. After skimming birds typically flew up and circled widely to make another pass on the windward (south) side of the pond, performing this behavior over and over again. The sky was clear, the temperature was 29°C, and the wind 8–13 km/h (measured by a Dwyer wind meter); the wind caused ripples on the surface of the turbid water. All birds on all passes flew directly into the wind while skimming. On the following day, when the air was nearly calm, no gulls were skimming on the pond during the two check periods although many individuals were flying about the area.

As is often the case with the evolution of unusual behavior patterns, the specialized skimming of the Rynchopidae appears to have recognizable phylogenetic precursors in the simpler skimming of related species in other charadriiform families. One other gull is known to skim: a single Black-headed Gull (*Larus ridibundus*) was observed by J. P. H. (*in* Buckley and Hailman, Br. Birds 63:210–212, 1970) to rotate its head ventro-posteriorly and snap its bill together during 1 of 11 skimming bouts. Skimming-like behavior in terns has been interpreted by P. A. Buckley (Buckley and Hailman 1970) and F. G. Buckley and P. A. Buckley (Ibis 114:344–359, 1972) as drinking when they skimmed after being flushed from the nest during the heat of the day or bill-cleaning following prey capture. None of these observations report wind conditions at the time of skimming or skimming-like behavior.

Skimming in Laughing Gulls thus shows little similarity to skimming-like behavior of terns, in that the gulls were neither cleaning their bills after capture of prey nor drinking when flushed from the nest at mid-day. Rather, skimming by gulls resembles foraging by skimmers, with an important proviso: Black Skimmers can skim in calm air whereas the strong head wind appeared to provide the necessary lift allowing skimming by Laughing Gulls.

We thank Robert Howe and Richard Zusi for valuable comments on the manuscript.—Jack P. Hailman and Jonathan R. Reed, *Dept. Zoology, Univ. Wisconsin, Madison, Wisconsin 53706.* *Accepted 31 Mar. 1981.*

Wilson Bull., 94(2), 1982, pp. 225–229

A lamp-booth for laboratory use.—The importance of using a reliable color standard for color evaluation is well known. Equally important is the quality of the light source under which it is used. Most artificial light sources, such as ordinary incandescent and typical daylight fluorescent lamps, are unsatisfactory for accurate color evaluation; some phase of natural daylight is usually preferred by people who work with color. Excellent simulated daylight enclosures and fixtures are available commercially, but often prove too costly for low-budget research projects.

Faced with unsuitable laboratory illumination as well as a restricted budget, I decided to devise a lamp-booth for use in my research on downy waterfowl. Two booths were built, using as a guide certain apparatus specifications in American Society for Testing and Materials pamphlet D 1729–69 (1974), "Standard method for visual evaluation of color differences of opaque materials." The larger booth (Fig. 1) has one pair of 48" (1219 mm) 40w 7400 K or 7500 K lamps, approximating north daylight, as well as an optional alternate pair of 48" 40w 5000 K lamps, approximating noon daylight (K = kelvin: unit of absolute temperature); the smaller booth, not shown, has two pairs of 24" (610 mm) 20w 5000 K lamps. Both booths have an optional, three-part curtain with head-sized viewing aperture (an accessory 45° viewing stage with styrofoam pinning surface for evaluating insect specimens is shown in a photograph of the larger booth by McKillop and Preston [Can.Entomol. 113:256,

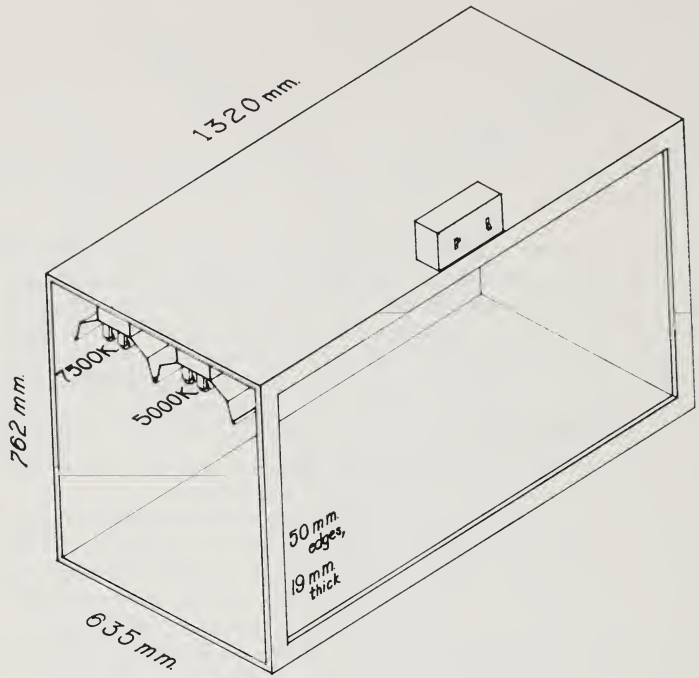


FIG. 1. Isometric drawing of larger booth, with side removed to show lamp placement. Curtain and 3.5 m electrical cord not shown.

1981]). All surfaces of the booths, including reflectors and viewing stand, were painted with Pratt and Lambert Vapex flat wall finish, color no. 2507, Crane Gray (Calibrated II Series), which has the Munsell value N 6.05/, with chroma less than /0.2 (Pratt and Lambert, F. J. Abel, in litt.). Color of the gray curtains was estimated visually as 5R 6.8/0.4.

Illumination of the booths was tested initially and at intervals thereafter with a Gossen model D P MT–2CC Photometer, Serial 310, manufactured by the Holophane Company, Ltd. In addition, illumination levels were checked at least once every 100 h with a Gossen "Lunasix 3" Exposure Meter. After the first 100 h of operation, the illumination level of the lamps decreased from approximately 200 foot-candles (2150 lumens/m^2) when the lamps were new to approximately 125 foot-candles (1340 lumens/m^2) at the time they were discarded. Note that this range of illumination is permissible for color evaluation, but not always for color matching, which involves additional criteria.

The selection of the lamps themselves is the first consideration in setting up an effective lamp-booth. The lamps should be cool, reasonably efficient and available; they should provide even illumination of an area large enough to contain and to manipulate specimens (including live material) and color standards. Most important, the spectral energy of the lamps should approximate that of a daylight phase or reference illuminant (e.g., a CIE [International Commission on Illumination] standard illuminant) of the same correlated color temperature (K) as closely as possible throughout the spectral range, so that colors evaluated under the lamps will appear much as they would under the daylight or reference illuminant. This

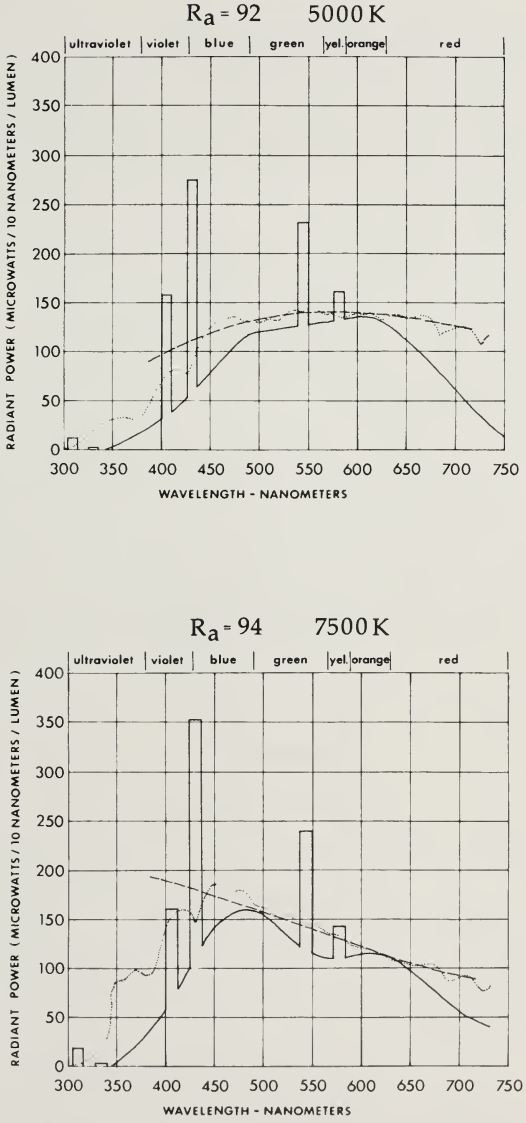


FIG. 2. Spectral energy distribution of 5000 K and 7500 K lamps, used in smaller and larger booths, respectively. Reference illuminants (.....): typical daylight at 5000 K and 7500 K (*from* CGE Lamp Letter LL4–72, Dec. 1972). Note: The abrupt bursts of energy at the wavelengths of the mercury emission lines are characteristic of all fluorescent lamps.

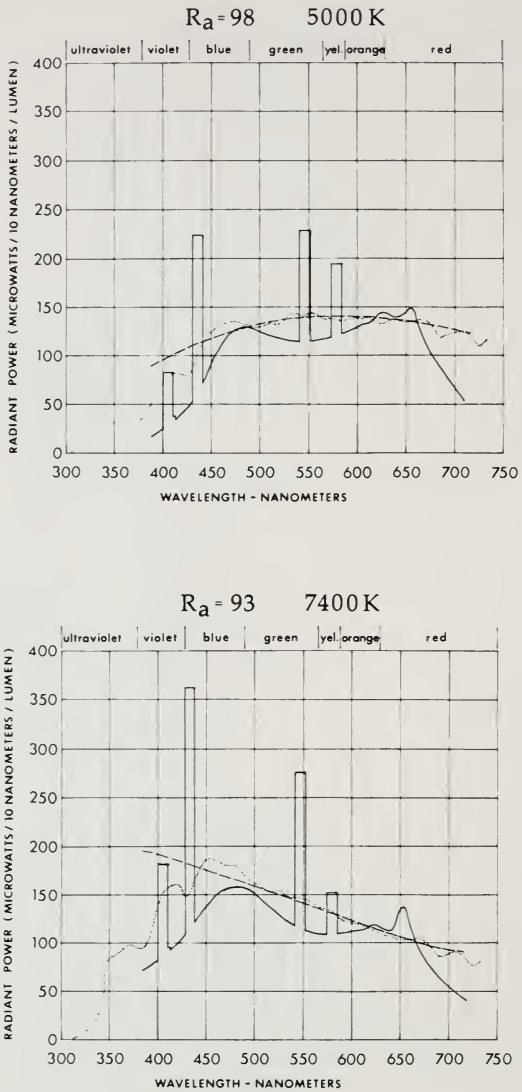


FIG. 3. Spectral energy distribution of 5000 K lamp used in larger booth (*from* Philips "Fluorescent Lamps" brochure). Spectral energy distribution of 7400 K lamp used alternatively in larger booth (*from* Philips Engin. Rept. 9, Lighting, 1968:23). Respective reference illuminants (dashes = optimized curve): black body (Planckian) radiator at 5000 K; reconstituted daylight at 7500 K (Philips Electronics, Lighting and Transformer Division, George Szeker, in litt.). Both drawings enlarged or altered to same scale as Fig. 2. See Fig. 2 Note.

correlation, called the color rendering index (R_a), should be close to 100 for accurate color evaluation. (See Appendix for more detailed discussion of color rendering and colorimetry.)

While the spectral energy distributions of the lamps selected (Figs. 2 and 3) suggest very good color rendering throughout the visible spectral range, the correlation with their respective reference illuminants is closest in the yellow and red wavelengths (ca. 575–650 nanometers), where most avian colors are found, e.g., 18 of the 21 most frequently used colors analyzed by Palmer and Reilly (A Concise Color Standard, A.O.U. Handbook Fund, 1956:5) and 55 of the 86 listed by Smithe (Naturalist's Color Guide, Pt. 1, Am. Mus. Nat. Hist., New York, New York, 1975:Intro.). Readers who wish to construct a lamp-booth and whose work involves evaluation of a particular range of colors should seek lamps that render these colors most accurately. All major lamp companies (General Electric, Philips, Sylvania, Westinghouse, etc.) manufacture deluxe or special daylight lamps and will provide technical data about them on request. These should include at least spectral energy distribution, both general (R_a) and individual (R_i) color rendering indices, color temperature and approximate initial lumens, so that the lamps chosen will be those best suited for the research intended.

I thank H. MacDiarmid for advice about and testing of the illumination of both lamp-booths, Carl and J. Nelson for building the smaller booth and G. Lammers for authorizing the construction of the larger booth by the museum workshop staff. I am grateful to H. MacDiarmid, R. Wrigley and B. McKillop for reading early drafts of the manuscript, to G. Wyszecki for reading critically a later draft and to G. Szeker for checking the drawings for Fig. 3. A. Einerson helped prepare Fig. 1 and Carl Nelson did the final drawings for Figs. 1, 2 and 3. Fig. 2 was redrawn with permission of Canadian General Electric Lamp Department and Fig. 3 with permission of Philips Electronics, Ltd., Lighting and Transformer Division.—Colleen Nelson, *Manitoba Museum of Man and Nature, Winnipeg, Manitoba R3B 0N2 Canada.* *Accepted 11 May 1981.*

APPENDIX

Suggested References

Besselaar, T. 1968. Colour appearance and colour rendering of fluorescent lamps. Engin. Rept. 9, Lighting. Philips, Eindhoven.

CIE Expert Committee E–1.3.1 (Colorimetry). 1971. Colorimetry: official recommendations of the International Commission on Illumination (G. Wyszecki, Chairman). Publication CIE No. 15 (E–1.3.1). Bureau Centrale de la CIE, Paris, France.

Judd, D. B. and G. Wyszecki. 1975. Color in Business, Science, and Industry. 3rd Ed. Wiley, New York, New York. (The sections, Fundamental standards in colorimetry, pp. 102–189, and Color rendering of light sources, pp. 362–368, are particularly recommended. Extensive bibliography.)

Wyszecki, G. 1970. Development of new CIE standards for colorimetry. Die Farbe 19:43–76. (Concerns testing of 35 artificial light sources for suitability for colorimetry.)

Wilson Bull., 94(2), 1982, pp. 230–238

ORNITHOLOGICAL LITERATURE

ELLIOTT COUES: NATURALIST AND FRONTIER HISTORIAN. By Paul R. Cutright and Michael J. Brodhead. Univ. Illinois Press, Urbana, Illinois, 1981:509 pp., 8 pp. of photos. $28.50.— With preparations for the 1983 centennial of the American Ornithologists' Union well under way, the appearance of this biography of one of the AOU's principal founders is timely. The book provides a sensitive and objective insight into the extraordinary life and character of one of the 19th Century's leading American zoologists. Although Coues is best known today for his extensive ornithological contributions, Cutright and Brodhead provide a comprehensive account of his involvement in other branches of natural history, as well as in theosophy, women's rights and the history of the American West.

Coues' passion for natural history was inspired by his mother, Charlotte Ladd Coues, who contributed lively essays on plants and animals to the "New Hampshire Gazette" in the 1850's. From her he also began to acquire the facility of expression that so characterized his writings. From the time of his early expedition to Labrador through his long service as an Army surgeon at numerous western and southern outposts, Coues made extensive natural history collections, primarily for the Smithsonian Institution. Throughout this time he wrote tirelessly to his early mentor, Spencer Fullerton Baird, and eventually to many others who became his colleagues and friends, among them J. A. Allen, William Brewster and John Burroughs. We are treated to numerous excerpts from these letters as well as from published articles, so full of keen observation and vivid verbal pictures of frontier life. During his first sojourn in Arizona Coues had occasion to skin an Arizona coral snake (*Micruroides euryxanthus*) on horseback "under the untoward circumstances of a hasty retreat from hostile Indians." Noteworthy is the contrast between the opportunities for comfortable birdwatching in the southwest today and conditions in Coues' time, in his words: "Practical ornithology in Arizona was a very precarious matter, always liable to sudden interruption [by Indians], and altogether too spicy for comfort." Coues published hundreds of articles and larger works on natural history, medicine, theosophy and history. One of the numerous honors bestowed upon him for his zoological work was a "Memorial" signed by 38 of Britain's leading scientists, among them Charles Darwin, Alfred Russell Wallace and Thomas Huxley.

The biography is written with that painstaking detail that makes history reality. Certain events in Coues' life were particularly intriguing and the authors do not disappoint the reader's instant longing for detail. As a young medical student Coues evidently engaged in occasional body snatching, and we learn thereby of the history of this grisly practice. We are also allowed details of Coues' numerous and occasionally illicit friendships with women.

A brilliant man who approached genius, Coues could be irascible, and he showed no mercy when fe felt that one of his colleagues had violated the rules of logic, grammar or spelling. Cutright and Brodhead, while highly respectful of their subject, do not attempt to defend him when his outbursts were unreasonable. If his personal faults lie undefended, however, his special kindnesses to his younger colleagues do not go unpraised, and we learn of the attention paid by Coues to his young protegé, Louis Agassiz Fuertes. Fuertes' extraordinary talents as an artist were in danger of being neglected, as his father thought engineering a more lucrative calling. When Coues' nephew, a friend of young Fuertes, brought the latter's work to his uncle's attention, Coues immediately recognized the potential of the artist and devoted considerable effort to the development of Fuertes' career as a painter of birds. One of his first steps was to arrange an exhibit of Fuertes' paintings at the 13th Congress of the AOU in 1895. The artist was 21 years old at the time, and his work "caused a furore" at the meetings.

I noticed a few inaccuracies in avian nomenclature. While for the most part giving current

scientific names and, often, enlightening explanations of common names, several changes appearing in the 32nd Supplement to the AOU Check-list (Auk 90:411–419) go unrecognized. These include use of the name *Hylocichla* for *Catharus*, *Richmondena* for *Cardinalis*, *Passerherbulus* for *Ammospiza* and *Rhynchophanes* for *Calcarius*. The authors cite this supplement and thus were certainly aware of the changes made; therefore, their failure to incorporate these changes into the manuscript can only be regarded as an oversight. In most cases, the authors were careful to provide current scientific names, both zoological and botanical, after those used by Coues if changes had been made since his day.

I experienced only one inconvenience in reading this book, viz., the lack of a chronology of Coues' life in the form of an appendix for quick reference; this sometimes necessitated a bit of skipping about in order to refresh one's memory. We are provided, however, with extremely valuable bibliographies: works both about Coues and by Coues, as well as a list of taxa described by him. The footnotes are a mine of information. With the introduction of each new character, no matter how minor a role the person played in Coues' life, we are provided with a few lines or more of biographical data. The footnotes also convey peripheral information of possible interest to the reader, such as attempts to give modern interpretations of medical symptoms described by Coues during the course of his medical service.

This careful and scholarly work will appeal to biologist, historian and layman alike. While written in an engaging style, it is unembellished with the fanciful speculation that so often characterizes popular accounts. The biography represents an impressive amount of research, and it is very clear that the authors found the work, as Coues so often said of his own extensive labors, "wholly congenial."—Mary C. McKitrick.

Birds of the North Solomons. By Don Hadden. Wau Ecology Institute (Wau, Papua New Guinea) Handbook No. 8, 1981:ix + 107 pp., 24 color plates, map. $9.50 postpaid (paper). Order from Bishop Museum Press, Box 1900–A, Honolulu, Hawaii 96819.—The Wau Ecology Institute, in the mountains of eastern Papua New Guinea, has been issuing an admirable series of handbooks, of which this is the eighth. Previous handbooks have covered New Guinea frogs, beetles and rodents; montane birds of NE New Guinea; ecology of Mt. Kaindi; biological terms in Melanesian Pidgin; and reptiles of the Solomon Islands. The North Solomons, the area covered by the new handbook, includes only Bougainville Island of World War II memory and the small adjacent island of Buka. These two are politically part of Papua New Guinea, whereas the rest of the Solomon Islands comprise an independent nation.

No true field guide published to date includes the birds of the Solomons. Land and fresh water birds were listed for each of the major islands or island groups and were briefly described by Mayr (Birds of the Southwest Pacific, 1945), but his book was minimally illustrated. Postwar advances in our knowledge of Solomons birds is indicated by Mayr's total of 89 species for Bougainville and by his statement that "There is not a single [Solomon] island on which one can expect to find more than 100 species." The Bougainville list of land and fresh water birds now totals over 100, and adding migrants, seabirds and shorebirds brings the list to over 150 species. Of these, 76 are illustrated in the new handbook by excellent color photographs by the author, who has conscientiously indicated which were taken elsewhere than in the Solomons (Papua New Guinea, Sarawak, New Zealand). In a few, the photographs are so reduced as to make them of little use for identification. In others, the birds were photographed in the hand or at close range from a blind; many are superb. Color reproduction seems adequate in most instances, although the subtle iridescence of the Glossy Swiftlet (*Collocalia esculenta*) has become a garish blue.

The text begins with a brief description of Bougainville and Buka, followed by lists of

species to be expected in various habitats. Then comes a history of the ornithology of these islands. For beginners who want to identify birds seen in easily accessible non-forest areas, Hadden gives descriptions of 24 of the most common species, arranged by habitat. Suggestions follow as to the best times and places to see birds on Bougainville and Buka. The species accounts occupy most of the book, followed by several appendices. Two are of special ecological interest, dealing with the effects on bird life of the large copper mines in the Crown Prince Range, and of the newly-formed delta at the mouth of the Jaba River, growing at the rate of 6–7 ha per month from sediments containing mining wastes (71 species have been seen on the delta, with nesting confirmed for six).

The species accounts contain descriptions (often but not always including voice), habitat, and total distribution of the species. A paragraph entitled "Field Notes" includes such miscellaneous information as feeding and flocking habits, breeding data, behavioral notes, etc. Each family has a one- or two-sentence general introduction.

The level of ornithological knowledge of the North Solomons can be deduced from the fact that Hadden includes excellent photographs of a bird, its nest and egg that were previously unknown to science. A formal description of the "Thicket Warbler" is said to be in press. Also intriguing is the "odedi," a bird well known to local natives, and readily heard (but never seen) by western observers at elevations of 850–1340 m, but not yet identified. All of the exciting discoveries are not just coming from Peru!

This little book is a model well worth emulating, and its author is to be congratulated. The price may seem a bit steep for a small paperback, but the fine illustrations and the uniqueness of its geographic coverage make it a good buy.—Kenneth C. Parkes.

Birds of Southern California. Status and Distribution. By Kimball Garrett and Jon Dunn. Illustrated by H. Lee Jones. Los Angeles Audubon Society, 1981:408 pp., maps, numerous line drawings. Order from L.A.A.S., 7377D Santa Monica Blvd., Los Angeles, California 90046. $18.95 plus $1.50 postage and handling. California residents add $1.14 sales tax.—Southern California is a region of great topographic and climatic variety, which is reflected in the diversity of its avifauna. In this book, Garrett and Dunn have combined to provide up-to-date and critically-evaluated information on the more than 500 species that have occurred there. The region treated is essentially the Southern Pacific coast region of "American Birds," but the authors also include summary information on 30-odd additional species that have been recorded in the northern half of the state. This is, then, a book on the birds of California.

No, of course it will not replace Grinnell and Miller's (1944) classic work on the avifauna of the state. As the authors point out, Grinnell and Miller painted an essentially complete picture of the breeding birds and racial distribution but knew little about the status of migrants and vagrants, information that has increased dramatically in the past two decades. Garrett and Dunn have managed to condense and interpret these new data in an attractive, informative manner, including information on habitats. They also provide critical data on the status of some well-defined races, appreciation of which has diminished with the decline of legitimate collecting and the re-emergence of lumping. Details of most records, names of observers and citations of the original literature are largely omitted, but will be provided on request.

The authors have done their homework. The taxonomic arrangement used is largely in accordance with that of the forthcoming AOU Check-list; nevertheless, it is a shock to find the loons hidden back with the Charadriiform assemblage.

The book is well balanced and only rarely strikes an alarmist tone. For example, it remains an open question whether the current commercial take of anchovies will affect the repro-

duction of Brown Pelicans (*Pelecanus occidentalis*), the least endangered of all species so classified.

If there is room for quibbles it is in the fluctuating standard of species accepted for inclusion. Mostly, the authors abide by decisions of the California Bird Records Committee. Yet, they list some species whose authenticity has not been judged, and some, which though accepted, are based on shaky evidence. I cannot understand the inclusion of the Parakeet Auklet (*Cyclorrhynchus psittacula*), known from decomposed specimens that may have washed in from afar, and the exclusion of Kittlitz's Murrelet (*Brachyramphus brevirostris*), known from a bird found alive on a beach.

In summary, this is a well-conceived and well-executed book, enhanced by the fine line drawings of H. Lee Jones. Perhaps better than any other recent book it illustrates the sophistication of well-trained birders and the ever-increasing contribution they are making to knowledge of the changing patterns of avian distribution. It is a strong addition to the regional literature and will be a standard reference for California for a long time.—J. R. Jehl, Jr.

The Cuckoo. By Ian Wyllie. B. T. Batsford Ltd., London; Universe Books, New York, New York, 1981:176 pp., 15 color plates, 35 black-and-white photos., with line drawings and tables. $30.00.—The Common Cuckoo (*Cuculus canorus*) is the bird best known in the world to be a brood parasite. For centuries Europeans have known it to lay eggs in the nests of other birds, which then rear the young. Nevertheless, it may not be the best-known parasitic bird. Shy and elusive, it has been described in most complete detail by Edgar Chance in Worcestershire, England. Chance wrote two books on his cuckoos, "The Cuckoo's Secret" (1922) and "The Truth About the Cuckoo" (1940). By finding all nests of the local host species, the Meadow Pipit (*Anthus pratensis*), Chance was able to anticipate the laying cuckoo and could take his colleagues into the field to watch the female arrive on schedule and lay her egg. His intimate knowledge of the cuckoo allowed him to recognize a female even though she was not color-marked, as her eggs were individualistic in color and spotting pattern. Later field workers have used the same means of identifying their birds by their eggs, and not until Ian Wyllie's study has a biologist followed the behavior of individually marked cuckoos. The present book summarizes much of what is known about other populations and cuckoo species of the world, reports Wyllie's field observations and gives a good series of photographs of cuckoos parasitizing a population of Reed Warblers (*Acrocephalus scirpaceus*) in Cambridgeshire.

Wyllie marked cuckoos with colored wing tags and with radio transmitters. He followed the behavior of individual tagged birds for five years (1975–1979), to determine territorial and social relations, and mating system. He also marked young cuckoos in the nest to determine whether they would return and lay eggs like those of their mothers, thus tracing the genetics of the egg mimicry and polymorphism.

"Reed Warbler Cuckoos" are spaced apart and the males sing and chase; individual females appear to be more territorial and exclusive than males. One female lays most of the cuckoo eggs in a local colony of Reed Warblers, but other females sometimes lay in the same colony and even in the same nest. Nearly all parasitized nests have only one cuckoo egg. In several cases, the apparently locally-dominant female removed the eggs of another female, then laid her own. In one population, three subordinate females lived in the active range of another apparently dominant female. Six males were present in the same area. Individual males were said to be recognizable by their songs; no audiospectrograms are shown, and in my experience song varies more with mood than with individuals. The primary laying female fed over a wide area, but mainly along a railway line 4–5 km from the warbler population that she

parasitized. Cuckoos generally ignored each other on the feeding area, and Wyllie suggests that this area was ecologically indefensible as the female spent much of her time in the laying area.

All male singing, and all attempted and observed matings were in the laying area, not the feeding area. Females were courted by more than one male. Wyllie observed only three matings, none involving marked pairs. Two of these involved a marked female mating with, apparently, one unmarked male on alternate days, then shortly thereafter laying in warbler nests. Wyllie concludes that cuckoos are not strictly territorial but may be organized in a loose social hierarchy within an area, and that they are probably promiscuous, no pairs travelling together. Social interactions among cuckoos deserve further field study.

Wyllie was able to confirm many of the observations that Chance had made in a different cuckoo population. Individual females laid almost exclusively in the nests of a single species of host. Females laid a variable number of eggs in a single season, sometimes quite a few: three "Reed Warbler Cuckoos" laid 1–12, 15 (twice) and 3–6 eggs in a season. Females laid every other day, over a period of several days, then took a break for a few days. The series, or clutches, in the best-known cuckoo were 8, 3 and 4 eggs. Cuckoos usually laid late in the afternoon.

Studies of the population structure of cuckoos had limited success. Wyllie had four cuckoos wing-tagged that returned to their home area in a later breeding season. Three were males; the female was seen only twice and did not stay and breed. The study did not determine whether daughters have eggs like their mothers' eggs. Wyllie did not compare his observations of young returning to their natal site in a later year with the larger number of observations of other banders showing that most young return to a site other than their natal site, usually more than 10 km away (Payne, Ann. Rev. Ecol. Syst. 8:1–28, 1977; Seel, Ibis 119:309–322, 1977). Given the dispersal of cuckoos in general, I was impressed by the number of young that did return. Wyllie wing-tagged 32 young cuckoos of at least 10 days of age from 1975–1978, so an appreciable proportion of young birds surviving did return in a later year. The cases of the returning birds suggest that the possible mother-daughter series of eggs over the years in local populations reported by others may have been correctly interpreted. However, the larger number of cuckoos that are genetically effective dispersers from their birth site gives us strong evidence opposing the idea that local cuckoo populations are inbred races or "gentes" in the sense of Southern (*in* Evolution as a Process, 1954). Although Wyllie does not discuss the proportion of dispersers and local returners, he does suggest that the egg mimetic polymorphism is likely transmitted genetically as a simple sex-linked trait passing from mother to daughter without involving locally coexisting races of cuckoos that do not inter-breed with each other (the "gens" concept). Wyllie does not critically evaluate the "gens" concept himself, but his observations of several males courting a female suggest promiscuous behavior, not assortative as required of the "gens" concept.

Other chapters in the book discuss cuckoos in general, host specificity among the cuckoo species, migration, food and songs. Wyllie suggests the hawk-like appearance of cuckoos may be an adaptation that reduces hawk predation, but he does not discuss the aggressive behavior of hawks towards each other that would nullify the plumage mimicry hypothesis nor how this "mimicry" may be related to parasitism. The material covered was spotty, and I found a number of statements that reflect a lack of intimacy on the part of the author with other species and areas. The book is more successful in describing the fieldwork with the marked cuckoos, though as the author is quick to note, we still have a lot to find out about them.

The photographs show mimicry and polymorphism of cuckoo eggs, egg-ejecting behavior of the young cuckoo upon hatching, egg predation of both the host eggs by breeding female cuckoos, and the tiny hosts feeding their oversized foster young. The author was first

stimulated to look at cuckoos by working with Maurice Tibbles during the making of his film, "The Private Life of the Cuckoo." Both that film and Wyllie's book are successful studies in the natural history of a curious bird, and the book is the best available source on behavior of the cuckoos.—ROBERT B. PAYNE.

YELLOWLEGS. By John Janovy, Jr. St. Martin's Press, New York, New York, 1980:192 pp. $9.95 (hard cover). Houghton Mifflin Co., Boston, Massachusetts, 1981, $5.95 (paper cover).—"Yellowlegs" is not a natural history of the Lesser Yellowlegs (*Tringa flavipes*), nor is it the fruit of any conventional research on this shorebird. It is the work of a man obsessed by the vision of what others might call an "ecological nightmare": mysteriously, the yellowlegs represents for Janovy both the natural world at the mercy of misguided technology, and a wondrous travelling machine that should command our respect. The Lesser Yellowlegs, and in fact, one individual of this species, becomes the symbol of what the author must learn about if he is to become an ecologist of conscience. On a self-granted sabbatical from his teaching duties as a professor of biology, Janovy decides to follow his chosen bird as far as he can, and the believability of his story, and its rather melodramatic conclusion hinges to some extent upon whether or not the banded yellowlegs he keeps sighting at various spots during its migratory flight within the United States is indeed one bird.

The factual aspects of the story are combined with sections that are more imaginitive, where, for example, Janovy muses about what his bird (a "she," he assumes) is doing, and thinking, as she travels across the technological landscape that we have created. Clearly there are long stretches during which the author can only follow his bird in his mind's eye. He then gives us portraits of some of the human characters he encounters during his own "flight south," and his book reads in large part like a rambling travel journal with philosophical asides. While lamenting the devastation that technological growth can cause, Janovy does not simplistically condemn technology. At the heart of his book is the realization that the machine concept can be applied to both human and natural products. Indeed, Earth is the "ultimate machine" for Janovy, and he worries about the fact that there is no sensible garage we can take it to in the future when it breaks down like an old Ford. Janovy is a critic of the misuse of machines, or rather of the lack of planning in their proliferation, and his nightmare is of "the world as a complicated machine driven by a species that doesn't know how to take care of it" (p. 32). The bird he has chosen to follow, the planet, and a second-hand car are all examples of beautiful machines for the author, and they all require an attitude of respect if they are to be treated properly. Using the hackneyed division between the "classic" and "romantic" perspectives, Janovy argues for the primacy of the latter. A "romantic" is someone who follows intuition (and, presumably, yellowlegs); a willingness to do so when dealing with very complicated machines implies a belief that these machines have an integrity that may not yield up its secret immediately to a "classic" approach that uses only a part-by-part analysis of the mechanism to understand it. What Janovy's position amounts to is the old faith that parts of the natural world are put together with delicacy and precision, however arrived at, and that we neglect this at our peril when we interfere in natural processes.

Janovy writes as if he is a talker, and an embellisher of tales. "Yellowlegs" is a stream of consciousness book, and suffers from the shifting perspectives that the author delights in. The reader can easily get lost and lose sight (as the author did during his quest) of the small, grayish bird that supposedly unifies the story. Janovy's rhapsodic style comes perilously close to being a parody of the poetry of Allen Ginsberg, replete with exclamation points: "The egg tooth was the technological equivalent of a monstrous controlled fire-bomb skyscraper Saturn rocket—used once to get into the world of flight then discarded!" ((p. 43).

In musing about what his bird is thinking, Janovy's writing is perhaps least successful, yielding such commonplaces as "She had no knowledge or understanding of a concept such as a rule" (p. 133), and, "She was simply a bird" (p. 125). It is difficult to follow the story line through meandering chapters, although this elusiveness might add to the charm of such a book for some readers. Clearly the author has had some sort of mystical experience, but at the end we come only to the conclusion that he is a sincere, enthusiastic teacher who discovered for himself the primacy of creative thought in a world increasingly technological. His intriguing promise to deal with how his yellowlegs negotiates its human-transformed environment in migration is really carried out only in imagination. Janovy is certain that his experience of trying to follow a migrating bird (by car) and discovering certain limitations has made him a better ecologist and a better teacher of biology. But, ultimately, the book is confusing in its details and frequently strains the reader's credulity. Janovy's insights are not new, but he has seen something important, and it does transform his attitude toward the natural world. One wishes that his message could have been more coherent. As it is, his book is almost as hard to follow as a migrating yellowlegs.—K. E. Duffin.

Annual Variation of Daily Energy Expenditure by the Black-billed Magpie: A Study of Thermal and Behavioral Energetics. By John N. Mugaas and James R. King. Studies in Avian Biology No. 5, Cooper Ornithological Society, 1981:78 pp, 20 tables, 14 figs. with captions. $8.00.—This book is more than just a study of the daily energy expenditure of the Black-billed Magpie (*Pica pica hudsonia*); it points out the importance of an integrated approach (combining ecology, physiology and behavior) to answering ecologically relevant questions. Over the past 10 years economic modeling (time-energy budgets) has become extremely popular among ecologists. The present study by Mugaas and King differs from preceding studies in that it deals with the magpie's time-energy budget throughout the year, whereas previous studies dealt mainly with one portion of the year, usually the reproductive season. As the authors point out it is the annual time-energy budget that allows one to determine what the bottleneck of energy or time is that puts limits on the survival or distribution of the species. The present study emphasizes the importance of the use of the microclimate by the magpie and points out the dangers of relating macroclimate to geographic distribution. Though this is not a new concept to physiological ecologists, the detailed analysis of the thermal environment, the behavioral responses to thermal stress, the energetic cost in the different microclimates and the cost of various behaviors greatly strengthens the concept.

The time-activity laboratory (TAL) method used in this investigation to determine total daily energy expenditure was shown to give reasonably accurate estimates as long as measured energy equivalents are available for the behavior being described and thermoregulatory demands are adequately determined. I agree with the authors that there are many pitfalls to using this method, mainly because of the large number of assumptions one must make. Theoretical calculations of the effect of forced convection on metabolic rate rather than actual measurements of the effects of wind on metabolic rate and variation in the cost of flight, to name a few, can introduce relatively large errors. The authors review the various TAL methods and compare them to the more expensive, more accurate D_2O^{18} method for estimating total daily energy expenditure, and point out the precautions one must take to use the TAL method.

The study described in this book is the most thorough investigation of daily energy expenditure of a bird in the literature and should be read by anyone interested in integrating behavior, physiology and ecology into an economic model of total energy expenditure.—Sheldon Lustick.

THE AUDUBON SOCIETY HANDBOOK FOR BIRDERS—A GUIDE TO LOCATING, OBSERVING, IDENTIFYING, RECORDING, PHOTOGRAPHING AND STUDYING BIRDS. By Stephen W. Kress. Charles Scribner's Sons, New York, New York, 1981:xiii + 322 pp., 172 figs. (black-and-white photos. or line drawings). $17.95.—As O. S. Pettingill, Jr., points out in the Foreword to this impressive introduction to field ornithology, the study of birds, both on a casual basis and from the view of advanced research, has enjoyed an enormous growth in the past several decades. Along with this there has been a concurrent increase in the technical and popular literature, the number and kinds of equipment, and the range of opportunities, both geographic and otherwise, for enjoying birds. This book is a remarkable summary of all of these facets, written to be useful to the amateur as well as the more advanced student.

The organization of the book roughtly parallels the progress of an individual from the beginnings of birding through the first approaches to technical research. The first chapter introduces methods for field study, including bird identification, how to approach and locate birds, and how to lead a bird walk. As with the subsequent chapters, Kress provides sufficient detail to be useful in a wide variety of situations but does not overwork the points he has to make. The second chapter deals with the topic of binoculars and spotting scopes, from technical details of the optics to suggestions on purchasing and use. Kress has obviously been teaching others about this equipment for a long time; this is the best treatment of the subject I have seen. Chapter three covers the beginnings of bird study: how to observe birds. Considerable space is devoted to the kinds of behavior likely to be encountered, and systems for recording field observations are emphasized. Another section covers sketching of birds in the field. If birders followed the procedures suggested here they would be well on their way toward publishing in the technical literature. Kress is an expert photographer and his fourth chapter covers in detail the photographing of birds. The discussion is limited to 35mm slide photography but many of the suggestions apply to motion picture making as well. As with the chapter on binoculars, technical details are included and the presentation of results (slide shows) is covered along with the equipment and techniques of photographing birds. The chapter concludes with a short section devoted to the equipment and techniques of sound recording. The remaining chapters (5–8) cover the educational and research opportunities open to amateurs as well as an introduction to the literature published in North America on birds. The number of bird courses, tours and research programs (chapters five and six) is impressive and covers all of the North America north of Mexico; the cooperation of the professionals in providing these data is commendable. Chapters seven and eight cover the ornithological organizations and their publications. As with the educational opportunities, the coverage is remarkably complete. In addition, Kress gives specific recommendations of books and journals for a variety of topics; they agree well with my own preferences. Finally, three appendices cover suppliers and retailers of birding equipment and books (Appendices A and B) as well as a list of publications available from natural resource agencies (Appendix C); I have often wished for such complete lists.

The book is well illustrated with black-and-white photographs (mostly from the author's collection) as well as excellent line drawings by Anne Senechal Faust. All appear to be carefully chosen and add considerable clarity to an already well-written text. Kress has succeeded in answering in print the myriad questions that have (I am sure) been posed to him by countless amateurs (and professionals). I have often had these same questions asked of (and by) me and I am very glad to have this reference, both to consult for myself and to suggest to others. I recommend it highly to all who spend time observing birds, whether they merely watch the backyard bird feeder or are engaged in sophisticated research questions.—D. SCOTT WOOD.

The Relationships of the Pedionomidae (Aves: Charadriiformes). By Storrs L. Olson and David W. Steadman. Smithsonian Contributions to Zoology No. 337, Smithsonian Institution Press, Washington, D.C., 1981:25 pp., 13 black-and-white figs. Price not given.—The Australian Plains-wanderer (*Pedionomus torquatus*) has been placed in a monotypic family close to the button quails, Turnicidae, now included in the order Gruiformes. Based largely on a phenetic study of osteology, Olson and Steadman conclude that *Pedionomus* should be transferred to the order Charadriiformes near the Thinocoridae.—R. J. R.

Variation in the Jaw Musculature of the Avian Family Vireonidae. By Ronald I. Orenstein and Jon C. Barlow. Life Sciences Contributions, Royal Ontario Museum No. 128, 1981:60 pp., numerous tables, charts and line drawings. $3.75 (Canadian). Order from Royal Ontario Museum, Publication Services, 100 Queen's Park, Toronto M5S 2C6, Canada.—The jaw musculature is compared in *Vireo*, *Hylophilus*, *Cyclarhis* and *Vireolanius*. One basic pattern occurs, but variations are related to differences in the feeding apparatus, foraging behavior and food type.—R. J. R.

Birds of a Feather: Unpublished Letters of W. H. Hudson. Edited by Dennis Shrubsall, Illustrated by Marcus Beaven. Moonraker Press, Bradford-on-Avon, Wiltshire, England. Distributed in U.S.A. by Buteo Books, Vermillion, South Dakota; 1981:108 pp., 10 plates. $16.—To readers familiar with W. H. Hudson's extensive writings these letters offer a somewhat surprising view of the author's life, for they reveal him as a sickly and sedentary man chained to city life rather than as the endlessly wandering adventurer we might imagine him to be.

The editorial remarks and footnotes, while useful, are insufficient to satisfy the reader's curiosity about some aspects of Hudson's life that are hinted at in his letters; the collection serves mainly as a companion to more thorough biographical treatments available elsewhere. The book has a pleasing format and is illustrated with numerous skillfully rendered wood engravings.—Mary C. McKitrick.

Wilson Bull., 94(2), 1982, pp. 239–240

ORNITHOLOGICAL NEWS

NORTH AMERICAN LOON FUND GRANTS

The North American Loon Fund (NALF) announces the availability of two grant programs for support of new or current research, management, or education projects that may yield useful information for Common Loon conservation in North America.

The first of these programs, the Robert J. Lurtsema Research Award, consists of a $1000 stipend available annually for a suitable research project focused on a member of the Family Gaviidae. Preference will be given to students and independent researchers with limited availability of other funding.

The second program offers modest grants in support of research, management, or educational projects directly related to the conservation of Common Loons as a breeding species. Proposals in the range of $500–3000 are most likely to be considered for funding.

Further guidelines for prospective applicants are available upon request from the NALF Grants Committee. Deadline for submission of proposals is 31 January 1983. Funding awards will be announced by 15 March.

Please submit guideline requests to North American Loon Fund Grants Committee, North American Loon Fund, Meredith, New Hampshire 03253.

HAWK MOUNTAIN RESEARCH AWARD

The Board of Directors of the Hawk Mountain Sanctuary Association announces its fifth annual award for raptor research. To apply for the $500 award students (undergraduate and graduate students enrolled in a degree granting institution) should submit a description of their research program, a curriculum vitae and two letters of recommendation by 31 October 1982, to Mr. James Brett, Curator, Hawk Mt. Sanctuary Association, Route 2, Kempton, Pennsylvania 19529. Projects will be selected on the basis of their relevance to conservation of North American hawk populations and ability to improve understanding of raptor biology. Final decision will be made in February 1983.

A.O.U. ANNUAL MEETING

The 100th Stated Meeting of The American Ornithologists' Union will be held 10–15 October 1982 in Chicago, Illinois. For further information on the scientific program write James R. Karr, Program Chairman, Dept. Ecology, Ethology and Evolution, University of Illinois, Champaign, Illinois 61820.

BEHAVIOR SYMPOSIUM

A symposium on "Optimizing behavior under ecological constraints: sex and food" will be held 11–14 November 1982, near Sherbrooke, Quebec, Canada, in conjunction with the annual meeting of Le Société Quebécoise pour l'Étude Biologique du Comportement. Dr. Jon Ericksen, SUNY, and Dr. Don Kramer, McGill University, will be guest speakers. Potential contributors or anyone interested in attending should contact Dr. André Cyr, Biology Dept., University of Sherbrooke, Sherbrooke, Quebec J1K 2R1 Canada. Abstracts should be sent no later than 15 September 1982.

BREEDING BIRDS IN CAPTIVITY SYMPOSIUM

The Jean Delacour/International Foundation for the Conservation of Birds Symposium on Breeding Birds in Captivity will be held 24–27 February 1983 at the Sheraton-Universal Hotel, Hollywood, California. The program will emphasize natural history as it applies to the future of captive birds, their husbandry and management. Dr. Jean Delacour will be one of the hosts, and over fifty international speakers will participate. For more information contact Delacour/IFCB Symposium, % Gary Schulman, 11300 Weddington St., North Hollywood, California 91601 (telephone [213] 980–9818).

BIRDS AND MAN: A SYMPOSIUM

The Witwatersrand Bird Club is holding a symposium on Birds and Man 10–15 April 1983, in Johannesburg, South Africa. International guest speakers have been invited; topics will include exotic birds in cities, indigenous birds in cities, indigenous birds and exotic plants, exotic birds and indigenous plants, birds and man-made lakes and bird/man interactions. Excursions are planned. For further information write to Symposium Secretary, P.O. Box 72091, Parkview, Johannesburg, 2122, South Africa.

RED-COCKADED WOODPECKER NEWSLETTER

The "Red-cockaded Woodpecker News," a newsletter dedicated to this endangered species is now available to interested individuals. Requests for subscription or further information should be sent to Anne Shapiro, Florida Game and Fresh Water Fish Commission, 620 South Meridian St., Tallahassee, Florida 32301 (telephone [904] 488–3831). The purpose of this newsletter is to summarize and promote the exchange of information about the conservation of the Red-cockaded Woodpecker.

ANNUAL MEETING—THE WILSON ORNITHOLOGICAL SOCIETY, 1983

Plan now to attend the 64th annual meeting of The Wilson Ornithological Society, 2–5 June 1983, at the University of Wisconsin at Green Bay, Green Bay, Wisconsin. The local chairman is Dr. Richard B. Stiehl, College of Environmental Studies, University of Wisconsin at Green Bay, Green Bay, Wisconsin 54302.

This issue of *The Wilson Bulletin* was published on 24 June 1982.

The Wilson Bulletin

Editor Jon C. Barlow

Department of Ornithology
Royal Ontario Museum
100 Queen's Park
Toronto, Ontario, Canada M5S 2C6

Associate Editor Margaret L. May

Assistant Editors Gary Bortolotti
Nancy Flood
Keith L. Bildstein

Senior Editorial Assistant Richard R. Snell

Editorial Assistants C. Davison Ankney
James D. Rising

Review Editor Robert Raikow
Department of Biological Sciences
University of Pittsburgh
Pittsburgh, PA 15260

Color Plate Editor William A. Lunk
865 North Wagner Road
Ann Arbor, MI 48103

Suggestions to Authors

See Wilson Bulletin, 91:366, 1979 for more detailed "Suggestions to Authors." Manuscripts intended for publication in *The Wilson Bulletin* should be submitted in triplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411–419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

Notice of Change of Address

If your address changes, notify the Society immediately. Send your complete new address to Ornithological Societies of North America, % Sandra L. L. Gaunt, Box 21160, Columbus, Ohio 43221.

The permanent mailing address of the Wilson Ornithological Society is: c/o The Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109. Persons having business with any of the officers may address them at their various addresses given on the back of the front cover, and all matters pertaining to the Bulletin should be sent directly to the Editor.

Membership Inquiries

Membership inquiries should be sent to Dr. Keith Bildstein, Department of Biology, Winthrop College, Rock Hill, South Carolina 29733.

CONTENTS

A NEW SPECIES OF ANTPITTA (*GRALLARIA*) FROM NORTHERN PERU
Thomas S. Schulenberg and Morris D. Williams 105

THE RELATIONSHIPS OF THE VIREOS (VIREONINAE) AS INDICATED BY DNA-DNA HYBRIDIZATION ---------- *Charles G. Sibley and Jon E. Ahlquist* 114

VEGETATION RELATIONSHIPS AND FOOD OF SAGE SPARROWS WINTERING IN HONEY MESQUITE HABITAT ---------- *Julie K. Meents, Bertin W. Anderson and Robert D. Ohmart* 129

ECOLOGICAL RELEASE AND ECOLOGICAL FLEXIBILITY IN HABITAT USE AND FORAGING OF AN INSULAR AVIFAUNA ---------- *Monique I. Vassallo and Jake C. Rice* 139

AVIAN NEST DENSITIES AND NEST-SITE SELECTION IN FARMSTEAD SHELTERBELTS
Richard H. Yahner 156

THE INFLUENCE OF SEASONALITY AND SELECTED WEATHER VARIABLES ON AUTUMN MIGRATION OF THREE SPECIES OF HAWKS THROUGH THE CENTRAL APPALACHIANS
Kimberly Titus and James A. Mosher 176

RADIONUCLIDES IN MOURNING DOVES NEAR A NUCLEAR FACILITY COMPLEX IN SOUTHEASTERN IDAHO ---------- *O. Doyle Markham and Douglas K. Halford* 185

GENERAL NOTES

GREAT BLUE HERON EGGSHELL THICKNESS AT OREGON ESTUARIES ------ *Range D. Bayer* 198

NESTING PHENOLOGY OF THE DOUBLE-CRESTED CORMORANT
James A. Kushlan and Linda C. McEwan 201

REPLACEMENT NESTING AND POLYANDRY IN THE WATTLED JACANA ---- *David R. Osborne* 206

HABITAT OF BACHMAN'S SPARROWS BREEDING ON MISSOURI GLADES
Kimberly I. Hardin, Thomas S. Baskett and Keith E. Evans 208

A DOUBLE-BROODED EASTERN KINGBIRD ------ *Peter J. Blancher and Raleigh J. Robertson* 212

MALE COOPER'S HAWK BREEDS IN JUVENAL PLUMAGE
Robert N. Rosenfield and Jonathan Wilde 213

UNUSUAL FEEDING BEHAVIOR BY A POPULATION OF BLACK VULTURES
Donald J. Elias and Danilo Valencia G. 214

CLAPPER RAIL PREYS ON SAVANNAH SPARROW
Paul D. Jorgensen and Howard L. Ferguson 215

COMMENSAL FEEDING OF LITTLE BLUE HERONS WITH MANATEES
Michael D. Scott and James A. Powell 215

COMPARISON OF THE NEST-SITE DISTRACTION DISPLAYS OF BLACK-CAPPED CHICKADEE AND WHITE-BREASTED NUTHATCH ---------- *Charles A. Long* 216

A REVIEW OF HYBRIDIZATION BETWEEN *SIALIA SIALIS* AND *S. CURRUCOIDES*
Richard C. Rounds and Hugh L. Munro 219

INTERSPECIFIC PLUMAGE SIMILARITY: THE MOCKINGBIRD AND LOGGERHEAD SHRIKE
Robert W. Ficken and Millicent S. Ficken 223

HEAD WIND PROMOTES SKIMMING IN LAUGHING GULLS
Jack P. Hailman and Jonathan R. Reed 223

A LAMP-BOOTH FOR LABORATORY USE ---------- *Colleen Nelson* 225

ORNITHOLOGICAL LITERATURE ---------- 230

ORNITHOLOGICAL NEWS ---------- 239

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 94, NO. 3 SEPTEMBER 1982 PAGES 241–432

MUS. COMP. ZOOL. LIBRARY
OCT 11 1982
HARVARD UNIVERSITY

THE WILSON ORNITHOLOGICAL SOCIETY

FOUNDED DECEMBER 3, 1888

Named after ALEXANDER WILSON, the first American Ornithologist.

President—Abbot S. Gaunt, Department of Zoology, Ohio State University, Columbus, Ohio 43210.

First Vice-President—Jerome A. Jackson, Department of Biological Sciences, P.O. Drawer Z, Mississippi State University, Mississippi State, Mississippi 39762.

Second Vice-President—Clait E. Braun, Wildlife Research Center, 317 West Prospect St., Fort Collins, Colorado 80526.

Editor—Jon C. Barlow, Department of Ornithology, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, M5S 2C6 Canada.

Secretary—Curtis S. Adkisson, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061.

Treasurer—Robert D. Burns, Department of Biology, Kenyon College, Gambier, Ohio 43022.

Elected Council Members—Richard C. Banks (term expires 1982); Mary H. Clench (term expires 1983); Helen Lapham (term expires 1984).

Membership dues per calendar year are: Active, $16.00; Student, $14.00; Sustaining, $25.00; Life memberships $250 (payable in four installments).

THE WILSON BULLETIN is sent to all members not in arrears for dues.

THE JOSSELYN VAN TYNE MEMORIAL LIBRARY

The Josselyn Van Tyne Memorial Library of the Wilson Ornithological Society, housed in the University of Michigan Museum of Zoology, was established in concurrence with the University of Michigan in 1930. Until 1947 the Library was maintained entirely by gifts and bequests of books, reprints, and ornithological magazines from members and friends of the Society. Now two members have generously established a fund for the purchase of new books; members and friends are invited to maintain the fund by regular contribution, thus making available to all Society members the more important new books on ornithology and related subjects. The fund will be administered by the Library Committee, which will be happy to receive suggestions on the choice of new books to be added to the Library. William A. Lunk, University Museums, University of Michigan, is Chairman of the Committee. The Library currently receives 195 periodicals as gifts and in exchange for *The Wilson Bulletin*. With the usual exception of rare books, any item in the Library may be borrowed by members of the Society and will be sent prepaid (by the University of Michigan) to any address in the United States, its possessions, or Canada. Return postage is paid by the borrower. Inquiries and requests by borrowers, as well as gifts of books, pamphlets, reprints, and magazines, should be addressed to: The Josselyn Van Tyne Memorial Library, University of Michigan Museum of Zoology, Ann Arbor, Michigan 48109. Contributions to the New Book Fund should be sent to the Treasurer (small sums in stamps are acceptable). A complete index of the Library's holdings was printed in the September 1952 issue of *The Wilson Bulletin* and newly acquired books are listed periodically. A list of currently received periodicals was published in the December 1978 issue.

THE WILSON BULLETIN
(ISSN 0043-5643)

The official organ of the Wilson Ornithological Society, published quarterly, in March, June, September, and December. The subscription price, both in the United States and elsewhere, is $20.00 per year. Single copies, $4.00. Subscriptions, changes of address and claims for undelivered copies should be sent to the OSNA, Cornell Laboratory of Ornithology, 159 Sapsucker Woods Rd., Ithaca, New York 14850. Most back issues of the *Bulletin* are available and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

All articles and communications for publications, books and publications for reviews should be addressed to the Editor. Exchanges should be addressed to The Josselyn Van Tyne Memorial Library, Museum of Zoology, Ann Arbor, Michigan 48109. Known office of publication: Department of Zoology, Ohio State University, 1827 Neil Avenue, Columbus, Ohio 43210.

Second class postage paid at Ithaca, New York and at additional mailing office.

© Copyright 1982 by the Wilson Ornithological Society

Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

Heads of Spix's Guan, *Penelope jacquacu* (upper),
White-winged Guan, *P. albipennis* (middle),
and Crested Guan, *P. purpurascens* (lower),
to show soft part colors. Painting by John P. O'Neill.

© John P. O'Neill - 1982

THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY

Published by the Wilson Ornithological Society

VOL. 94, NO. 3 SEPTEMBER 1982 PAGES 241–432

Wilson Bull., 94(3), 1982, pp. 241–259

SYSTEMATIC RELATIONSHIPS AND ZOOGEOGRAPHY OF THE WHITE-WINGED GUAN (*PENELOPE ALBIPENNIS*) AND RELATED FORMS

J. WILLIAM ELEY

The avian genus *Penelope* (Cracidae), comprising 13–15 species (depending on the authority), is widely distributed from northeastern Mexico south to Argentina and Uruguay. Relationships within this genus are obscure, as reflected by the variation in recent taxonomic treatments (Vuilleumier 1965, Vaurie 1968, Delacour and Amadon 1973). There is general agreement by these authors that members of the genus fall into several species groups, although the exact composition and arrangement of these groups are also debated. Vuilleumier (1965) divided the genus into four species groups, and included species of *Pipile* in *Penelope*. Vuilleumier's (1965) conclusion that there are only eight species of *Penelope* (including *Pipile*) was not accepted in two subsequent treatments of the family. Vaurie (1968) and Delacour and Amadon (1973) generally agreed that the genus is divisible into one group of small species (*P. montagnii* [Andean Guan], *P. argyrotis* [Band-tailed Guan], *P. barbata* [Bearded Guan], *P. marail* [Marail Guan], *P. ortoni* [Baudó Guan], and *P. superciliaris* [Rusty-margined Guan], and two groups of large-sized species (*P. purpurascens* [Crested Guan], *P. jacquacu* [Spix's Guan], *P. obscura* [Dusky-legged Guan], *P. dabbenei* [Red-faced Guan], and *P. albipennis* [White-winged Guan] forming one group; and *P. pileata* [White-crested Guan], *P. ochrogaster* [Chestnut-bellied Guan], and *P. jacucaca* [White-browed Guan] the second).

Although all authorities have agreed that *P. albipennis* is most closely related to the *P. purpurascens-jacquacu* complex, there has been little speculation on its phylogenetic history. *P. albipennis* was thought to be extinct until its rediscovery in 1977, and the lack of a sufficient number of specimens and natural history information on the species made spec-

ulations on its affinities extremely tenuous. New information available on *P. albipennis*, including its vocalizations, has facilitated a systematic study of this species and its closest congeners. In this paper I examine the relationships within several of the large species of *Penelope* and present a model for the speciation of these forms during the Pleistocene.

P. dabbenei was not included in this study due to the scarcity of specimens and information on its natural history. It is considered by most workers to be an isolated subtropical zone relative of *P. obscura*.

DISCOVERY, DISTRIBUTION AND CURRENT STATUS OF *P. ALBIPENNIS*

P. albipennis was described in 1877 by Taczanowski from a specimen collected by Stolzmann in mangroves near the mouth of the Río Tumbes in northwestern Peru (Taczanowski 1877). A second specimen, a female, was taken a month later by Jelski at the Hacienda de Pabur near the town of Piura. This female was accompanied by two chicks, one of which was captured alive and raised, and became the third known specimen of *P. albipennis* (Vaurie 1966a). The species was considered rare by Stolzmann (Ogilvie-Grant 1896), and despite attempts by Maria Koepcke to find the bird in the 1950's and 1960's and by Gustavo del Solar in the 1970's, it was not seen or collected again until September 1977, when a small population was found by del Solar and John P. O'Neill at San Isidro, northeast of Olmos, near the Lambayeque-Piura border. O'Neill and del Solar were alerted to the presence of the species when a local farmer produced two birds which he had shot near his farm. Subsequent work has shown that the currently known range of *P. albipennis* lies entirely in the Dept. Lambayeque, from east of Ñaupe south to near Chongoyape, east of Chiclayo (Enrique Ortiz T., pers. comm.). In the past it probably extended from the Ecuadorian border south to the Río Chicaina [=Chicama?] in La Libertad (a range that coincides with the previous extent of suitable habitat) (Delacour and Amadon 1973). The species inhabits the dry wooded slopes and ravines of the western foothills of the Andes from ca. 300–500 m elev. (see Williams 1980). Because the first specimens were taken at the mouth of the Río Tumbes, *P. albipennis* may well have occurred in coastal gallery forests; its restriction to the Andean foothills is probably due to hunting pressure along the coast (Williams, pers. obs.). The current population size is difficult to estimate, but *P. albipennis* probably numbers fewer than 100 birds (John P. O'Neill and Enrique Ortiz, pers. comm.).

TAXONOMIC HISTORY

The first taxonomic treatments of *P. albipennis* (Ogilvie-Grant 1896, Peters 1934) considered the species allied to *P. ortoni* of the west slope of the Andes of Colombia and Ecuador. Peters (1934) and Vuilleumier

(1965) speculated that *P. albipennis* represented a partial albino of *P. ortoni*, despite the fact that Stolzmann (*in* Ogilvie-Grant 1896) reported seeing other birds with white wings. Hellmayr and Conover (1942) pointed out that *P. albipennis* is much larger than *P. ortoni* and questioned their close relationship. Vaurie (1966a:10, 1968), who reviewed the taxonomic history in detail, pointed out that Stolzmann was a "reliable and painstaking" observer and stated that his accounts of seeing other white-winged birds were probably accurate. This evidence combined with size and plumage differences between *P. albipennis* and *P. ortoni* led Vaurie (1968) to conclude that *P. albipennis* was a distinct species, but he did not speculate on its taxonomic affinities. Delacour and Amadon (1973) also discounted the hypothesis of Peters and Vuilleumier and stated that although the affinities of the White-winged Guan were unknown, it was probably related to *P. purpurascens* or *P. jacquacu*.

REVIEW OF RELATED FORMS

The following is a review of the species thought to be most closely related to *P. albipennis*. A map of their distributions is given in Fig. 1.

P. purpurascens (Crested Guan).—This species ranges from Tamaulipas in eastern Mexico and southern Sinaloa in western Mexico south through Central America, and in South America west of the Andes to the cordilleras north of Zaruma, Ecuador, and in the Magdalena Valley of Colombia to the headwaters of the Río Magdalena. Crested Guans also occur eastward across Venezuela, north of the Orinoco to its delta (Delacour and Amadon 1973). There is clinal geographic variation from north to south. The amount of rufous in the plumage increases, while the amount of white edging of feathers of the mantle and overall size decrease. Nonetheless, three subspecies are recognized (Delacour and Amadon 1973).

P. purpurascens is primarily a bird of lowland and lower montane rain forest, but is not restricted to dense forests. Throughout its range *P. purpurascens* also frequents subtropical forests up to 2700 m and occurs in the drier areas of western Mexico and Central America (Slud 1964, Dickey and van Rossem 1938).

P. jacquacu (Spix's Guan).—This species ranges from Guyana through Venezuela south of the Orinoco, in western Brazil east to the upper Tapajos and Rio Xingu, south to Para and northern Mato Grosso. It is also found in the eastern parts of Colombia, Ecuador, and Peru and into northern Bolivia (Delacour and Amadon 1973). Spix's Guan is found most often in tropical forests, locally up to 1360 m (AMNH 115876, Peru, Dpto. San Martin). Several Ecuadorian specimens examined had the notation "subtropical zone." The four subspecies recognized by Delacour and Amadon (1973) differ slightly in size, plumage hue, amount of white on certain

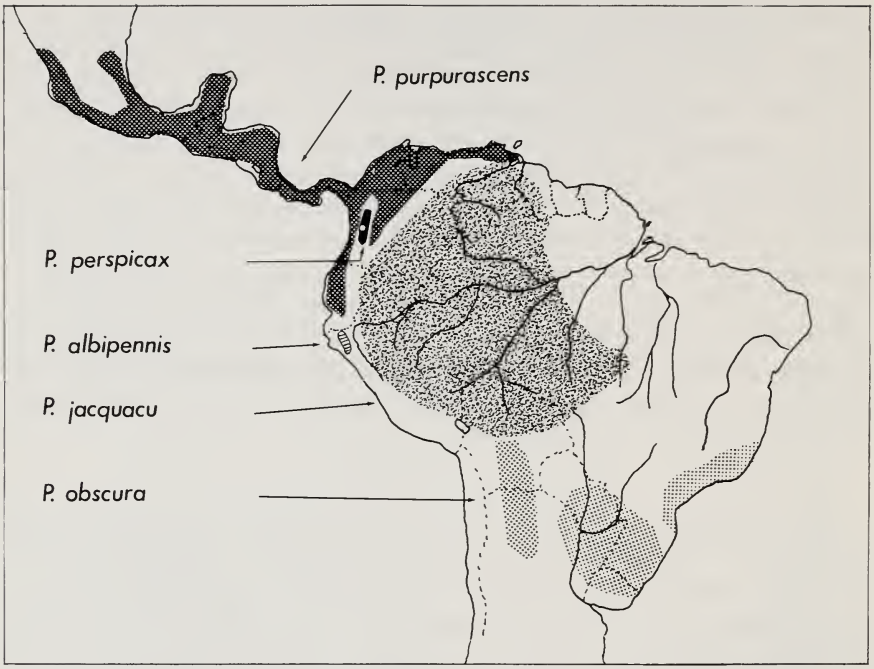


FIG. 1. Ranges of five closely related species of *Penelope* (from Vaurie 1968).

feathers, and shape of the crest. There is considerable intergradation between the races.

P. perspicax (Cauca Guan).—This guan is restricted to the subtropical slopes of the western Andes and eastern slopes of the central Andes in the Cauca Valley of Colombia (Delacour and Amadon 1973). There is controversy over the taxonomic status of the Cauca Guan. Vaurie (1966a) considered it a subspecies of *P. jacquacu*, citing similarities in the white edgings of certain shoulder feathers and the wing-tail ratio. Delacour and Amadon (1973) treated it as a full species and stated that its relationships lie with *P. purpurascens*, mainly because both lack a tracheal loop. Hellmayr and Conover (1942) considered the plumage differences to be of subspecific importance only, and listed *P. perspicax* as a zonal representative of *P. purpurascens*.

P. obscura (Dusky-legged Guan).—*P. obscura* occurs in three disjunct populations: one in eastern Brazil from Espirito Santo, Río de Janeiro, and southeastern Minas Gerais south through São Paulo and Parano to Santa Catarina; the second from southeastern Brazil in Río Grande do Sul west to northeastern Argentina, Paraguay and Uruguay; and the third from

central Bolivia south to northwestern Argentina (Vaurie 1968). The three subspecies recognized by Delacour and Amadon (1973) differ in coloration, size, and amount of white on the crest feathers. No intergradation between races has been demonstrated. Vaurie (1968) believed the distributional gap between the two western races to be a secondary modification of the range caused by an increase in aridity of the Chaco, which isolated the ancestral form into two allopatric populations.

The Dusky-legged Guan is found in tropical zone forest and also in montane areas up to 2000 m (ANSP 162364, Bolivia, Dpto. Chuquisaca) where lower elevations are too dry for evergreen forest (Delacour and Amadon 1973). The Bolivian race (*bridgesi*) is most often found at higher elevations, especially where its range approaches that of *P. jacquacu*.

TAXONOMIC CHARACTERS

Previous workers have not agreed on which taxonomic characters should be used to distinguish the Cracidae at the species level. The family is diverse in plumage, internal morphology, behavior and vocalizations, but the genera are delimited by conspicuous sets of characters. Most species of *Crax* (including *Mitu*), for example, possess a casque, frontal protuberance, or some modification of the bill. All members of *Penelope* have a wattle, dewlap, or areas of naked skin on the throat, and species of *Ortalis* exhibit uniformity in plumage pattern, voice, tracheal structure and tendency to polygamy (Vuilleumier 1965).

Within *Penelope* researchers have used a variety of characters to define species limits. Peters (1934) and Hellmayr and Conover (1942) considered various features of external morphology (absolute measurements and plumage pattern) sufficient to delineate closely related species. Vuilleumier (1965) stated that due to the overall clinal variation in the *P. purpurascens-jacquacu-obscura* group, no more than a single species should be recognized. Vaurie (1968) used body proportion, shape of the crest, tarsus color, or a combination of these characters in his analysis. Blake (1955) made the observation that there was no one character that separated *P. purpurascens* from *P. jacquacu*, and concluded that the two were conspecific, a view he no longer holds (Blake 1977). Blake did not suggest merging *P. obscura* with this group, as did Vuilleumier (1965), because he considered the black tarsus and different body proportions of *P. obscura* important specific characters. Delacour and Amadon (1973) believed that the wing-tail proportions used by Vaurie as a specific character were unimportant, and stated that the fact that *P. jacquacu* had a tracheal loop and *P. purpurascens* did not should be weighed heavily. The value of this taxonomic character is not clear and its possible significance is discussed in the following section.

The tracheal loop in the Cracidae.—The family Cracidae shows an unusual amount of variation in the modification of the trachea (Delacour and Amadon 1973). The function of a lengthened trachea is twofold: to impede higher frequencies (thus lowering the pitch of the call), and to increase volume (Clench 1978). In all chachalacas (*Ortalis*) a loop is present in males, but not in females, and this is associated with the loud, raucous calls characteristic of the group. Curassows show some variation between and within genera. *Nothocrax*, noted for its booming song, has a long tracheal loop, as does the Helmeted Curassow (*Pauxi pauxi*, sometimes considered *Crax*), which has a low, droning call (Delacour and Amadon 1973). Members of the *Crax rubra* (Great Curassow) superspecies have a tracheal loop, but in a reduced form. There is a peculiar flattening in the trachea of these species which may serve the same function as a long loop.

The situation in guans is more complex. In *Penelope*, six species have a loop, but four species do not. When present, there is some variation in its degree of modification. In the more aberrant guans (*Aburria, Chamaepetes, Penelopina* and *Pipile*), there is no tracheal loop. Delacour and Amadon (1973) speculated that the absence of a loop might be related to the whistled song of those groups, and that perhaps the trend in guans is toward the loss of the modified trachea and the "crowing" calls associated with it. The unusual Horned Guan (*Oreophasis derbianus*) also lacks a tracheal loop, although it has a low "mooing" call, reminiscent of the booming of the curassows. Vuilleumier (1965) considered the aberrant guans to be closer to the ancestral form. He stated that they have conserved some of the "primitive" characters such as very arboreal habits, ecological association with humid forests, and lack of patterned plumage. This might lead one to speculate that lack of a tracheal loop is also a primitive condition, but the evidence seems too meager to support such a conclusion.

Although the tracheal loop is a variable character among the species of *Penelope*, its presence or absence seems consistent within a species. Tracheal loops are used to modify voice, which is likely to be an important isolating mechanism in cracids. It is probable that voice, presence or absence of a loop, and wing-whirring displays form an important suite of characters for classifying this group at the species level.

SIZE DIFFERENCES IN *PENELOPE* AND THE PROBLEM OF *P. ORTONI*

Peters (1934) and Vuilleumier (1965) considered *P. albipennis* (a large species) to be closely related to *P. ortoni* (a small species) of the Pacific lowlands of Colombia and Ecuador south to Guayaquil. Vuilleumier (1965) noted that six birds collected from one population of *P. ortoni* in Colombia had some white areas scattered throughout the plumage, and he considered *P. albipennis* to be a similar partial albino. It is now known that

presence of white wings in *P. albipennis* is the normal condition. The partial albino hypothesis can be discounted. Nevertheless, the possibility that *P. albipennis* is closely related to *P. ortoni* must be considered.

Vaurie (1966b) stated that differences between *P. albipennis* and *P. ortoni* in size and in coloration of the crest indicate that the two species are probably not closely related. The mean wing and tail length obtained for *P. ortoni* males by Vaurie (1968) was 269.3 ± 8.5 mm and 235.8 ± 11.3 mm, respectively (24 specimens measured). For males of *P. albipennis* both wing and tail average 337 mm. No two species of *Penelope* considered closely related show size differences of this magnitude. Vaurie (1968) also stated that *P. ortoni* does not vary geographically. Since size seems to be an important character in delineating relationships at the species level in *Penelope*, it seems unlikely that an isolated population of *P. ortoni* could become one-third larger than "normal" *P. ortoni*.

Chapman (1917, 1926) lists *P. ortoni* as a representative species of the Colombian-Pacific fauna of western Colombia and Ecuador, and points out this avifauna is strikingly unlike the equatorial-arid fauna found farther south. He states also that this Colombian-Pacific avifauna was derived from Amazonia before the final uplift of the Andes, and that its isolation and differentiation was due to Pleistocene orographic events. Haffer (1967) agreed that most of the birdlife of the Colombian-Pacific fauna was derived from Amazonia but he suggested that it had crossed the northern end of the Andes at the beginning of the Pleistocene before the final uplift of the Andes. He stated that the isolation of this fauna was due to repeated wet-dry climatic cycles during the Pleistocene that created forest refugia in western Colombia.

The above evidence and speculation lead me to suggest that *P. ortoni* was derived from an ancestral stock that moved into western Colombia from Amazonia during the Pleistocene. Its nearest living relative appears to be *P. marail* of southern Venezuela and northern Brazil. The two species are similar in size (in males of *P. marail* the wing averages 281 mm and the tail 253 mm), and both share a dull, unpatterned plumage. It seems likely that the ancestral proto-*P. marail-ortoni* form had a wide distribution over much of tropical South America during the Pleistocene, and that climatic fluctuations, according to the model proposed by Haffer (1967), enhanced the formation of at least three species: *P. ortoni*, *P. marail*, and *P. superciliaris* a similar-sized species found south of the Amazon in Brazil, Paraguay and northeastern Argentina.

SPECIATION MODELS FOR *P. ALBIPENNIS*

The avifauna of southwestern Ecuador and northwestern Peru displays a 35% level of endemism (58 of 166 species are endemic), more than the

Santa Marta Mountains of Colombia (9.9%) and the Pantepui of Venezuela (30.2%) (Vuilleumier 1975). In his study of this avifauna, Chapman (1926) concluded that almost half (23 of 57 in his analysis) of the endemic species were derived from forms from the interior of South America. Only eight were thought to have been derived from Central American forms; the remaining 26 were of uncertain affinities. *P. albipennis*, the most differentiated of the large species of *Penelope*, should be included in Chapman's equatorial-arid fauna. At the time of Chapman's work in the 1920's, *P. albipennis* was thought to be extinct or nearly extinct and was not included in his analysis.

The two latest treatments of the Cracidae (Vaurie 1968, Delacour and Amadon 1973) have implied that *P. albipennis* was derived from *P. purpurascens* or *P. jacquacu*. These authors did not speculate on how this derivation of *P. albipennis* might have occurred. Haffer (1974) has offered explanations for the mechanisms of species formation during the Pleistocene and for many of the distribution patterns observed in birds in South America today. The following are three models proposed by Haffer for other species groups that may be relevant to the origin and speciation of *P. albipennis*. (1) Early in the Pleistocene, a widespread, undifferentiated proto-*P. purpurascens-jacquacu* ancestral population was divided by the rising Andes and subsequent climatic changes into five forms which today are the species *P. purpurascens*, *P. jacquacu*, *P. perspicax*, *P. albipennis* and *P. obscura*. *P. albipennis* would not be more closely related to *P. purpurascens* or *P. jacquacu*, but to the common ancestor of both. (2) *P. purpurascens* and *P. jacquacu* were once a widespread, undifferentiated single species that had a continuous distribution over Central and South America (extending into northern Peru). This ancestral form was separated early in the Pleistocene by climatic changes (Haffer 1974) and the rising Andes, which resulted in two incipient species (proto-*P. purpurascens* and proto-*P. jacquacu*). Later in the Pleistocene, a proto-*P. albipennis* was probably isolated from the proto-*P. purpurascens* stock in northwestern Peru. (3) In the late Pliocene or early Pleistocene, *P. purpurascens* and *P. jacquacu* were a widespread, undifferentiated single species. Climatic changes in the Pleistocene and the rising Andes separated the proto-*P. purpurascens* stock in northwestern South America. As the Andes reached their present height, the proto-*P. albipennis* was isolated in northwestern Peru from a westward extension of the proto-*P. jacquacu* stock. The southern limit of proto-*P. purpurascens* at this time was probably not as close to proto-*P. albipennis* as it is today.

Thus in model 1, *P. albipennis* is not any more closely related to *P. purpurascens* than to *P. jacquacu*; in model 2, *P. albipennis* is more closely related to *P. purpurascens* than to *P. jacquacu*; and in model 3, *P. albipennis* is more closely related to *P. jacquacu* than to *P. purpurascens*.

ANALYSIS OF MORPHOMETRIC DATA

Two recent taxonomic treatments of *Penelope* (Vaurie 1968, Delacour and Amadon 1973) have been based upon some aspect of morphometrics in addition to overall plumage pattern. Usually this consisted only of delimiting certain measurements, such as range and mean length of wing, tail, tarsus and exposed culmen, and then making taxonomic conclusions based on qualitative evaluation of these data. For example, Vaurie (1968) calculated the mean, range and standard deviation of wing, tail, tarsus and bill length of all species of cracids and used these descriptive statistics to support his phylogeny for the family.

Prior to the present study, a simultaneous assessment of a number of characters has not been attempted for the Cracidae. Multivariate analysis of six characters used in this study show how *P. purpurascens*, *P. jacquacu* and *P. obscura* fall into natural groupings according to mensural data, and why these natural groups might reflect phylogeny.

METHODS

The statistical analysis was based on measurements from specimens of *Penelope* from the Louisiana State University Museum of Zoology (LSUMZ), the American Museum of Natural History (AMNH), the Academy of Natural Sciences of Philadelphia and the U.S. National Museum (USNM). Six measurements were taken from each specimen: wing chord, length of tail, length of tarsus, length of culmen from anterior portion of the nostril, height of culmen at anterior edge of the nostril, and width of culmen at anterior edge of the nostril. If a specimen showed excessive wear in any of these characters, that character was not measured on that specimen. *P. albipennis* and *P. perspicax* were not included in the analysis due to inadequate sample size. Only those specimens of *P. purpurascens*, *P. jacquacu* and *P. obscura* from which all six measurements were taken could be used in the analysis.

These mensural data were analyzed using a multivariate analysis of variance (MANOVA) (Kendall and Stuart 1961) for the six characters for each sex to test for significant differences between species (overall species effect). Since the northern subspecies of *P. purpurascens* is noticeably larger than the southern, and since *P. albipennis*, if derived from *P. purpurascens*, would almost certainly be closely related to the southern one, the MANOVA was run twice, eliminating the specimens of the northern subspecies from the second analysis.

A discriminant analysis (Sneath and Sokal 1973) was used on the six characters for each sex to obtain pairwise squared generalized distances between *P. purpurascens*, *P. jacquacu* and *P. obscura* (Mahalanobis distance). Again, I used only specimens for which all six measurements were available. Nine specimens of *P. perspicax* were classified in the analysis as one of the three species used in the discriminant analysis to determine which species of *Penelope* it most closely resembled morphologically (posterior probability of membership) (Kendall and Stuart 1961).

RESULTS

The MANOVA comparison, using Wilk's Lambda criterion (Timm 1975) of *P. purpurascens*, *P. jacquacu* and *P. obscura* (including all subspecies of *P. purpurascens*) to test for no overall species effect showed that all three species were highly significantly different ($P \leq 0.01$) in the six char-

TABLE 1
MAHALANOBIS DISTANCES FOR THREE SPECIES OF *PENELOPE*

Males	Generalized squared distance to		
From	*P. jacquacu*	*P. obscura*	*P. purpurascens*
P. jacquacu	—	14.84	31.78
P. obscura	13.22	—	28.53
P. purpurascens	28.19	43.19	—
Females	**Generalized squared distance to**		
From	*P. jacquacu*	*P. obscura*	*P. purpurascens*
P. jacquacu	—	28.16	34.58
P. obscura	12.17	—	36.59
P. purpurascens	26.77	104.58	—

acters using either sex. Since eliminating the larger, northern subspecies of *P. purpurascens* did not affect the results of the tests, all subsequent data given include all subspecies of *P. purpurascens*.

The generalized squared distances between species are given in Table 1. In the procedure used, the Mahalanobis distance between groups (in this case, the species) is measured from the outer edge of one group hyperspace to the innermost point of another group hyperspace. Because the univariate character variation of the three species used here is not the same, the distances between any two hyperspaces are not "symmetrical," i.e., the distance between *P. jacquacu* to *P. obscura* is not the same as that between *P. obscura* and *P. jacquacu*. Nevertheless, it is clear that the *P. obscura* is consistently closer to *P. jacquacu* than to *P. purpurascens*. A classification summary posterior probability of membership (Kendall and Stuart 1961) into each species is given in Table 2. The high percentages of specimens correctly classified indicate that there is little overlap among the species in the six-dimensional space. Of nine specimens of *P. perspicax* identified as one of three taxa used in the discriminant functions analysis, eight were classified as *P. jacquacu* and one as *P. obscura*. This indicates that *P. perspicax* is morphometrically more similar to *P. jacquacu* than to either *P. obscura* or *P. purpurascens*.

Results of the previous analysis indicate that the four species of *Penelope* examined differ significantly in size. Mayr (1969) cautioned that significant size differences in species could bias the results of analysis of mensural data. Since the species considered in this analysis are of roughly the same size, there is considerable overlap in the mensural data, which

TABLE 2

POSTERIOR PROBABILITY OF MEMBERSHIP AND PERCENT CLASSIFIED INTO EACH SPECIES FOR THREE SPECIES OF *PENELOPE*

Males	No. of observations and percents classified into:			
From	*P. jacquacu*	*P. obscura*	*P. purpurascens*	Total
P. jacquacu	34	1	1	36
	94.44	2.78	2.78	100.00
P. obscura	0	10	0	10
	0.00	100.00	0.00	100.00
P. purpurascens	1	0	36	37
	2.70	0.00	97.30	100.00

Females	No. of observations and percents classified into:			
From	*P. jacquacu*	*P. obscura*	*P. purpurascens*	Total
P. jacquacu	23	2	0	25
	92.00	8.00	0.00	100.00
P. obscura	0	9	0	9
	0.00	100.00	0.00	100.00
P. purpurascens	0	0	25	25
	0.00	0.00	100.00	100.00

statistically minimizes the size-related bias. When the results of the previous statistical analysis are examined, certain trends between the species are apparent. *P. purpurascens* and *P. jacquacu* are distinct. *P. obscura* is also distinct, but much more similar to *P. jacquacu* than to *P. purpurascens*. *P. perspicax* is also very similar to *P. jacquacu*, as evidenced by the high probability of its classification as *P. jacquacu* in eight of nine specimens. Tables 3 and 4 show that *P. jacquacu*, *P. obscura*, and *P. perspicax* also share a wing-tail ratio of less than 1.

ANALYSIS OF VOCALIZATIONS

Vocalizations of birds of the genus *Penelope* are poorly documented. The recorded species are known to be highly vocal and to possess a wide variety of call and alarm notes. Most species of *Penelope* have three basic vocalizations: a loud alarm "scream"; a soft *whit whit* given either to maintain contact with conspecifics or as a mild alarm call given in the presence of an intruder; and a species-specific "yelping" call used in delineating territories (Paul Schwartz, in litt.). The following is a comparison of the various calls of *P. purpurascens*, *P. jacquacu* (recorded by P.

Table 3

Mean, SE, and Range for Six Characters of Males of Five Species of *Penelope*

Characters	N	*P. jacquacu*	N	*P. obscura*	N	*P. albipennis*	N	*P. perspicax*	N	*P. purpurascens*
Bill length	53	16.48 ± 0.152 (13.45–18.56)	13	15.83 ± 0.267 (14.57–17.81)	0	—	4	17.48 ± 0.158 (17.07–17.73)	64	17.59 ± 0.155 (14.59–20.04)
Bill width	61	8.42 ± 0.072 (7.25–9.73)	13	8.70 ± 0.23 (7.30–9.76)	0	—	4	8.92 ± 0.226 (8.30–9.36)	71	9.16 ± 0.070 (7.22–9.99)
Bill height	63	7.70 ± 0.070 (6.21–9.04)	13	8.17 ± 0.19 (6.73–9.30)	0	—	4	7.64 ± 0.09 (7.43–7.84)	71	7.98 ± 0.073 (6.17–9.50)
Tail length	46	331.83 ± 2.594 (300.00–369.00)	10	326.80 ± 8.546 (289.00–370.00)	1	325.00	4	333.75 ± 6.524 (315.00–345.00)	43	369.37 ± 4.479 (328.00–446.00)
Wing length	63	315.90 ± 1.993 (282.00–353.00)	12	317.67 ± 9.447 (253.00–356.00)	1	336.00	4	315.00 ± 4.243 (307.00–325.00)	70	379.60 ± 2.223 (341.00 ± 419.00)
Tarsus length	63	82.45 ± 0.477 (69.35–93.60)	12	81.23 ± 1.459 (73.30–90.90)	1	90.00	4	80.95 ± 1.584 (76.63–84.23)	68	85.21 ± 0.445 (75.85–95.52)
Wing-tail ratio		0.95		0.97		1.03		0.94		1.03

TABLE 4

MEAN, SE, AND RANGE FOR SIX CHARACTERS OF FEMALES OF FIVE SPECIES OF *PENELOPE*

Characters	N	*P. jacquacu*	N	*P. obscura*	N	*P. albipennis*	N	*P. perspicax*	N	*P. purpurascens*
Bill length	33	15.29 ± 0.280 (11.05–19.1)	12	15.33 ± 0.456 (12.60–17.96)	1	16.15	5	15.54 ± 0.483 (13.80–16.40)	49	17.01 ± 0.266 (7.50–19.50)
Bill width	36	8.11 ± 0.100 (6.75–9.34)	12	8.09 ± 0.284 (6.75–9.99)	1	9.36	5	8.23 ± 0.131 (7.85–8.62)	54	9.00 ± 0.083 (7.80–9.90)
Bill height	36	7.02 ± 0.103 (5.87–8.65)	12	7.50 ± 0.232 (6.05–8.79)	1	7.40	5	7.42 ± 0.158 (6.80–7.69)	55	7.72 ± 0.085 (6.45–9.60)
Tail length	30	319.03 ± 3.263 (290.00–374.00)	9	319.33 ± 7.599 (289.00–345.00)	2	342.50 ± 17.50 (325.00–360.00)	5	326.60 ± 5.784 (310.00–340.00)	33	367.64 ± 5.311 (316.00–424.00)
Wing length	38	300.21 ± 2.820 (260.00–347.00)	11	308.09 ± 7.288 (282.00–351.00)	2	337.00 ± 12.00 (325.00–349.00)	5	305.40 ± 3.669 (293.00–315.00)	56	370.30 ± 2.718 (327.00–410.00)
Tarsus length	37	79.30 ± 0.524 (72.90 ± 86.01)	12	78.51 ± 1.429 (69.55–87.15)	2	79.50 ± 1.50 (78.00–81.00)	5	77.59 ± 1.053 (74.88–80.15)	52	83.85 ± 0.562 (76.14–94.72)
Wing-tail ratio		0.94		0.97		0.98		0.94		1.01

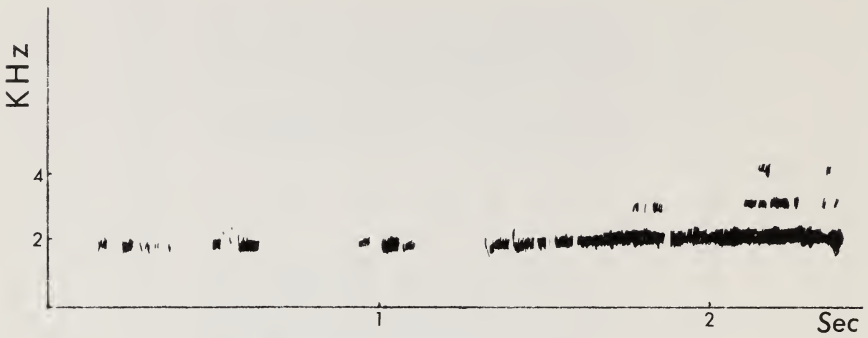


FIG. 2. Sonograms of "trumpeting" call of *P. jacquacu*.

Schwartz) and *P. albipennis* (recorded by T. Parker), and a discussion concerning the possible taxonomic significance of the similarities and differences. The sonograms presented in this study were prepared using a Voice Identification System Analyzer Model No. 700. Tracings were made of the original sonograms to eliminate excess background noise.

The "yelping" call, or a variation thereof, is found in all three species. In *P. jacquacu*, "yelping" is replaced by a call consisting of loud "trumpeting," which is often preceded by a series of low, introductory notes (Fig. 2). Occasionally, "trumpeting" is uttered softly, and it resembles the "yelp" of *P. purpurascens* and *P. albipennis*. "Trumpeting" of *P. jacquacu* seems to have the same function as the "yelping" call of *P. purpurascens* and *P. albipennis*, and is probably associated with the presence of a tracheal loop (P. Schwartz, in litt.). The "yelping" calls of *P. purpurascens* and *P. albipennis* are similar (Fig. 3). In both species, the call is softer than "trumpeting" of *P. jacquacu*, and usually has a faster cadence. It is noteworthy that neither species has a tracheal loop (Delacour and Amadon 1973; Gustavo del Solar, in litt.). These rapid calls are often preceded by a low growling that rises in pitch to become the plaintive "yelp."

An additional call shared by the three species is a short, low-pitched *whit*, given repetitively. The call is basically the same among the three species, and is probably used either to indicate mild disturbance or to maintain contact with conspecifics (Delacour and Amadon 1973).

Other studies have shown that similar vocalizations in groups of birds are reliable indicators of relationship (Johnson 1963, Lanyon 1978). The "yelping" calls of *P. purpurascens* and *P. albipennis* are much more similar to each other than either is to "trumpeting" of *P. jacquacu*. This suggests a close phylogenetic relationship between *P. purpurascens* and *P. albipennis*. The reasons for modification of this call in *P. jacquacu*,

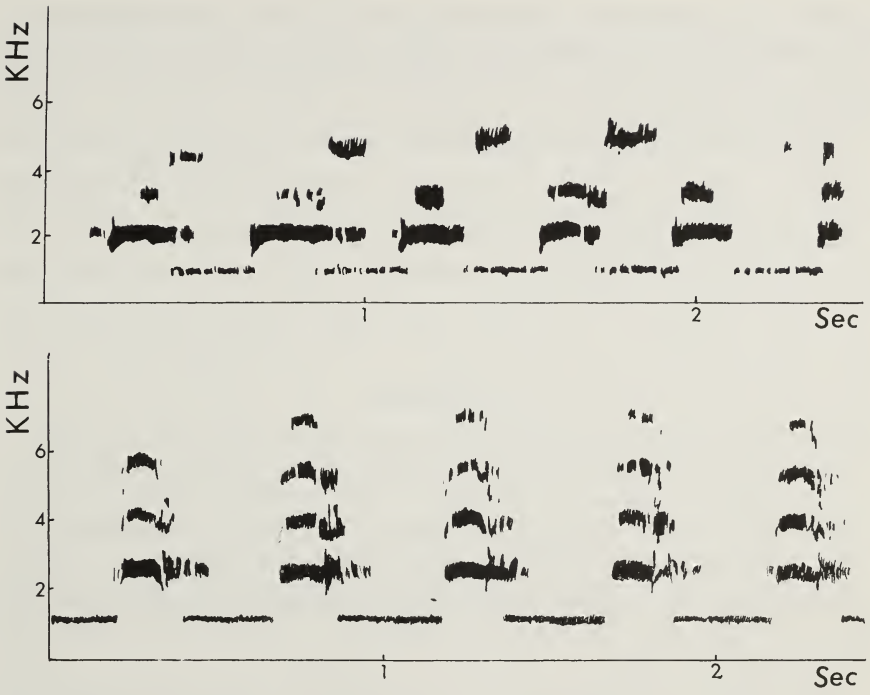


FIG. 3. Sonogram of "yelping" calls of *P. purpurascens* (above) and *P. albipennis* (below).

and its associated changes in tracheal structure, are not apparent. A possible explanation could be that in many parts of the Amazon Basin there are up to five (or possibly six) species of sympatric cracids (Delacour and Amadon 1973). The presence of several related sympatric species could have selected for increased vocal divergence through development of a tracheal loop. It is known that the loud, crane (*Grus*)-like "yelp" of *P. jacquacu* is completely unlike the calls of any other cracid in South America. An alternative explanation would be the possibility that all *Penelope* once had a tracheal loop, now lost in those forms inhabiting areas where fewer cracids are found.

DISCUSSION

My data show that certain morphological, distributional and behavioral trends are apparent within several species of *Penelope*. *P. purpurascens* and *P. albipennis* are vocally more similar to each other than either is to the other species found east of the Andes, namely *P. jacquacu* and *P. obscura*, both of which have a tracheal loop and are morphometrically

similar in six characters. *P. perspicax* is said to lack a loop (a living specimen examined by C. Lehmann, *in* Delacour and Amadon 1973), but it appears to be much closer to *P. jacquacu* in morphometrics and overall plumage coloration.

P. albipennis and *P. purpurascens* possess more unique characters than *P. jacquacu* and *P. obscura*. The bushy crest and large size of *P. purpurascens* set it apart from the other species and prompted Vaurie (1968:192) to state that *P. purpurascens* is "the most aberrant member of this complex" (*P. jacquacu*, *P. purpurascens*, and *P. obscura*). Vaurie did not include *P. albipennis* in his analysis because the species was known from only three specimens at the time of his study. *P. albipennis* possesses three unique characters: white primaries, a bicolored bill (blue, with a black tip), and a dark, greenish-gray plumage. The facial skin is also rosy slate in color instead of the bluish slate found in the other large *Penelope*.

With the above evidence one may evaluate the speciation models presented earlier in this paper. In model 1, all the species of *Penelope* are equally related and so the species would not exhibit the morphological and vocal trends shown by the data in this study. If model 3 was correct, *P. albipennis* and *P. jacquacu* should appear similar in vocalizations, and both should be different from *P. purpurascens*. This model is also not supported by the data.

The simplest explanation for the speciation of *P. albipennis* seemingly would be that encompassed by model 2. Proto-*P. purpurascens* and proto-*P. jacquacu* were separated early in the Pleistocene (or late in the Pliocene) and evolved the morphometric and vocal differences apparent between the two modern species. Later in the Pleistocene, proto-*P. albipennis* became isolated from the proto-*P. purpurascens* stock in northwestern Peru during one of the alternating wet-dry climatic cycles of western South America documented by Campbell (1979). Isolation in a new habitat type and subsequent contact with *P. purpurascens* during these climatic cycles possibly favored the development of white primaries in *P. albipennis* as a display character. Since the wing-whirring displays of *Penelope* occur above the tree tops in the twilight just before dawn, the increased visibility of white primaries in an open habitat would presumably be selectively advantageous.

The speciation of *P. perspicax* presents an interesting problem. The crest feathers of *P. perspicax* are intermediate between those of *P. purpurascens* and *P. jacquacu* (Delacour and Amadon 1973). Although *P. perspicax* is similar to *P. purpurascens* in some plumage characteristics (Delacour and Amadon 1973), it resembles *P. jacquacu* in others (Vaurie 1968). *P. perspicax* is similar to *P. purpurascens* in lacking a tracheal loop, but

is morphometrically closer to *P. jacquacu*. The confusing mosaic of characters of *P. perspicax* strongly suggests that it has diverged less from the putative common ancestral form than have *P. jacquacu* and *P. purpurascens*. *P. perspicax* may have arisen from the isolation of a population of the ancestral form in the Cauca Valley before the differentiation of *P. purpurascens* and *P. jacquacu*.

P. obscura and *P. jacquacu* are clearly more closely related to each other than to the other species of *Penelope* in plumage, morphometrics and tracheal loop morphology. *P. obscura* was probably isolated from the proto-*P. jacquacu* stock in the Pleistocene in one of the forest refuges of eastern Brazil (see Haffer 1974).

SUMMARY

Lowland guans of the genus *Penelope* (*purpurascens* group) in South America were studied to determine relationships within the group and present a speciation model for its members. New data available for the White-winged Guan (*P. albipennis*) provide insight into its phylogeny and speciation. A multivariate analysis of variance on six characters of *P. purpurascens*, *P. jacquacu*, *P. perspicax*, and *P. obscura* indicates that *P. jacquacu* and *P. purpurascens* are significantly different from each other in six characters, and that *P. perspicax* and *P. obscura* are more similar to *P. jacquacu* than to *P. purpurascens*. Analysis of vocalizations shows that *P. albipennis* calls are more similar to those of *P. purpurascens* than to those of *P. jacquacu*. Three speciation models proposed for *Penelope* were evaluated in light of the above data. The selected model proposed that *P. albipennis* was isolated in western Peru after the differentiation of a proto-*P. purpurascens* from proto-*P. jacquacu*. *P. perspicax* shared characters with both *P. purpurascens* and *P. jacquacu*, and was postulated to be closer to the ancestral form. *P. obscura* was clearly more closely related to *P. jacquacu* and was probably isolated in a forest refugium in eastern Brazil.

ACKNOWLEDGMENTS

I wish to thank the following persons for valuable discussions concerning this project: G. L. Graham, G. R. Graves, T. A. Parker, III, H. D. Pratt, T. S. Schulenberg and R. H. Vaeth. Special thanks are due J. P. O'Neill, J. V. Remsen and Gustavo del Solar for their help and encouragement. Manuel Plenge kindly measured the two specimens of *P. albipennis* for me in Lima. M. D. Williams, G. R. Graves, J. C. Barlow, and F. Vuilleumier provided comments on the manuscript. Sonograms were provided by the Cornell Laboratory of Ornithology. Travel to the American Museum of Natural History, the Academy of Natural Sciences of Philadelphia, and the U.S. National Museum of Natural History was facilitated by a grant from the Frank M. Chapman Memorial Fund. I also thank the curators at these institutions for allowing me to study specimens in their care.

The fieldwork was carried out under the auspices of the Louisiana State University Museum of Zoology. John S. McIlhenny, Babette M. Odom, and H. Irving and Laura R. Schweppe generously provided funds for the expeditions of which I was a part. I am grateful to Eric Cardich B., Antonio Brack E., Susana Moller H., Carlos Ponce P., Richard Bustamante M., and others in the Dirección General Forestal y de Flora of the Ministerio de Agricultura in Lima who helped in many ways.

LITERATURE CITED

Blake, E. 1955. A collection of Colombian game birds. Fieldiana: Zool. 37:9–23.

———. 1977. Manual of neotropical birds, Vol. 1. Univ. Chicago Press, Chicago, Illinois.

Campbell, K. E. 1979. The non-passerine Pleistocene avifauna of the Talara Tar Seeps, northwestern Peru. Royal Ont. Mus., Life Sci. Contrib. 118.

Chapman, F. 1917. The distribution of birdlife in Colombia; a contribution to a biological survey of South America. Bull. Am. Mus. Nat. Hist. 36.

———. 1926. The distribution of birdlife in Ecuador; a contribution to a study of the origin of Andean birdlife. Bull. Am. Mus. Nat. Hist. 55.

Clench, M. 1978. Tracheal elongation in birds-of-paradise. Condor 80:423–430.

Delacour, J. and D. Amadon. 1973. Curassows and related birds. Am. Mus. Nat. Hist., New York, New York.

Dickey, D. R. and A. J. van Rossem. 1938. The birds of El Salvador. Field Mus. Nat. Hist., Zool. 23.

Haffer, J. 1967. Speciation in Colombian forest birds west of the Andes. Am. Mus. Novit. 2294:1–57.

———. 1974. Avian speciation in tropical South America. Nutt. Ornithol. Club. 14.

Hellmayr, C. and B. Conover. 1942. Catalogue of birds of the Americas, Pt. 1, No. 1. Field Mus. Nat. Hist., Zool. 13:114–197.

Johnson, N. K. 1963. Biosystematics of sibling species of flycatchers in the *Empidonax hammondii-oberholseri-wrightii* complex. Univ. Calif. Publ. Zool. 66:79–238.

Kendall, M. G. and A. Stuart. 1961. The advanced theory of statistics, Vol. 2. Hafner, New York, New York.

Lanyon, W. E. 1978. Revision of the *Myiarchus* flycatchers of South America. Bull. Am. Mus. Nat. Hist. 161:429–627.

Mayr, E. 1969. Principles of systematic zoology. McGraw-Hill, St. Louis, Missouri.

Ogilvie-Grant, W. R. 1896. A handbook of game birds, Vol. 1. *In* Curassows and related birds (J. Delacour and D. Amadon, eds.). Am. Mus. Nat. Hist., New York, New York.

Peters, J. L. 1934. Checklist of the birds of the world, Vol. 2. Harvard Univ. Press, Cambridge, Massachusetts.

Slud, P. 1964. The birds of Costa Rica: distribution and ecology. Bull. Am. Mus. Nat. Hist. 128:1–430.

Sneath, P. and R. R. Sokal 1973. Numerical taxonomy. W. H. Freeman and Co., San Francisco, California.

Taczanowski, L. 1877. Supplement a la liste des oiseaux recueillis au nord du Perou occidental par M. M. Jelski et Stolzmann. Pp. 744–753 *in* Proc. Zool. Soc. London.

Timm, N. H. 1975. Multivariate analysis, with applications in education and psychology. Brooks/Cole Publ., Monterey, California.

Vaurie, C. 1966a. Systematic notes on the bird family Cracidae. No. 6. Reviews of nine species of *Penelope*. Am. Mus. Novit. 2251:1–30.

———. 1966b. Systematic notes on the bird family Cracidae. No. 5. *Penelope purpurascens*, *P. jacquacu*, and *P. obscura*. Am. Mus. Novit. 2260:1–23.

———. 1968. Taxonomy of the Cracidae. Bull. Am. Mus. Nat. Hist. 138.

Vuilleumier, F. 1965. Relationships and evolution within the Cracidae (Aves, Galliformes). Bull. Mus. Comp. Zool. 134:1–27.

———. 1975. Zoogeography. Pp. 421–496 *in* Avian biology, Vol. 5 (Donald S. Farner and James R. King, eds.). Academic Press, New York, New York.

Williams, M. D. 1980. First description of the eggs of the White-winged Guan, *Penelope albipennis*, with notes on its nest. Auk 97:889–892.

MUSEUM OF ZOOLOGY, LOUISIANA STATE UNIV., BATON ROUGE, LOUISIANA 70893. (PRESENT ADDRESS: DEPT. BIOLOGICAL SCIENCES, LOUISIANA STATE UNIV. IN SHREVEPORT, SHREVEPORT, LOUISIANA 71115. ACCEPTED 15 AUG. 1981.

COLOR PLATE

The color plate Frontispiece of the heads of Spix's Guan (*Penelope jacquacu*), White-winged Guan (*P. albipennis*), and Crested Guan (*P. purpurascens*) has been made possible by an endowment established by George Miksch Sutton. The painting is by J. P. O'Neill.

RESEARCH GRANTS

The Eastern Bird Banding Association and the Western Bird Banding Association are each offering research grants of $250 in aid of research using bird banding techniques or bird banding data. Applicants should submit a resume of his or her banding or ornithological background, the project plan, and a budget to the Joint Selection Committee Chairman: Robert C. Leberman, Powdermill Nature Reserve, Star Route South, Rector, Pennsylvania 15677. No formal application forms are available, and the amount requested should not exceed $250. The deadline for receipt of applications is 15 March 1983.

The Birmingham Audubon Society offers grants of less than $500 from the Walter F. Coxe Research Fund for the purpose of initiating research projects in any area of endeavor which has clear applicability to environmental issues. Projects should be related to Alabama, although need not be carried out there. Graduate students and others without access to other funding are invited to apply. For further information write to Charles Duncan, Walter F. Coxe Research Fund, Birmingham Audubon Society, P.O. Box 314, Birmingham, Alabama 35294.

NEW JOURNAL

The Colonial Waterbird Group announces the availability of its new journal, Colonial Waterbirds, which replaces Proceedings of the CWG. Future volumes of Colonial Waterbirds will include papers not necessarily presented at the Group's annual meetings, as in the past. All papers submitted will be subject to page charges and peer review.

This publication, as well as the Newsletter, are a benefit of membership ($20 individuals, $25 families), or it can be obtained from the Treasurer for $20 US. Back issues of the Proceedings ($12 US) can also be ordered from the Treasurer, Iola Price, 564 Fairview Ave., Ottawa, Ontario K1M 0X4 Canada. For further information about membership contact Francine Buckley, Secretary, 372 South St., Carlisle, Massachusetts 01741.

Wilson Bull., 94(3), 1982, pp. 260–268

ON THE MATING SYSTEM OF BROWN-HEADED COWBIRDS

C. Davison Ankney and D. M. Scott

The mating system of Brown-headed Cowbirds (*Molothrus ater*; hereafter called cowbirds) is poorly understood. Cowbirds have been reported to be monogamous (Laskey 1950, Darley 1968, Rothstein 1972), monogamous and polyandrous (Friedmann 1929), polygynous (Payne 1973), and promiscuous (Nice 1937, Elliot 1980). There is also disagreement about whether or not yearling males obtain mates (or copulations) (Payne 1973, Darley 1978). These uncertainties have prompted the suggestion that different geographic populations may have different mating systems (Elliot 1980, West et al. 1981a). We think it is more likely that these differences are more apparent than real and have resulted from observer bias.

Several aspects of the social and reproductive biology of cowbirds are reasonably well known: (1) the sex ratio of breeding birds is 1.5 (or more) males to 1 female (Friedmann 1929, Darley 1971, Payne 1973, Rothstein et al. 1980); (2) adult and yearling males court females and guard them from other males (Darley 1968, Rothstein 1972); (3) yearling males produce sperm (Scott and Middleton 1968, Darley 1968) and are as likely as adults to obtain mates in a laboratory situation (Darley 1978); (4) some males copulate with more than one female and some females copulate with more than one male (Elliot 1980); (5) dominant males pair (Darley 1978) and copulate (West et al. 1981b) more often than subordinates under controlled conditions; and (6) females defend territories but males do not (Darley 1968).

Wittenberger and Tilson (1980:Hypothesis 3) proposed that monogamy should evolve in any nonterritorial species if males can reproduce most successfully by defending access to a single female; they suggested that this was particularly true when sex ratios are male biased as in the case of cowbirds. They realized, from reviewing the literature, that the cowbird mating system was complex and proposed that it might involve both monogamy and promiscuity.

In this paper, we report new data about cowbird social groups and use these data, and those summarized above, to hypothesize about the mating system of cowbirds. Our hypothesis is similar to that proposed by Wittenberger and Tilson (1980), but is based largely on different assumptions, interpretations and data about cowbirds.

METHODS

During a study of the fecundity and nutrient-reserve dynamics of cowbirds, we collected 115 males in the breeding season in 1976. Breeding season is here defined as time from when the first laying female was collected (29 April) until before the date (7 July) that the first post-laying female was collected; on 7 July we began collecting at feedlots where social groupings could not be determined and many males and females were out of breeding condition. No laying females were collected after 7 July. Birds were collected within 50 km of London, Ontario; to avoid potential bias associated with repeated sampling of a local population, we collected in a different area each week (each collection area was >8 km from all other such areas). Details of collecting are in Scott and Ankney (1979) and Ankney and Scott (1980). Birds were weighed in the field (to nearest 1 g) and the social group from which each came was recorded. We distinguished four social groups: (1) 'alone'—no other cowbirds detected nearby; (2) 'paired'—with a female; (3) 'male group'—with one or more males; and (4) 'mixed party'—with one or more males and females. The overall proportions of males which we collected from each social category likely did not reflect the true proportion of all males in those categories. That is because we intentionally collected more females than males (20 vs 15 each week) for our research about fecundity and nutrient reserves. This meant that, for example, when a pair was encountered the female was the primary target and the male was collected only if it did not disappear at the first shot, and if the weekly quota of males had not been met. Males were probably most likely to be collected as singles or from male groups but this would not affect the probability of an adult or yearling being collected from a particular social group, i.e., if the true proportion of adults and yearlings did not differ between social groups, they would not differ in our sample. Males were classed as adult or yearling according to the criteria of Selander and Giller (1960). This method is not 100% accurate as some yearlings are indistinguishable from adults, but there is no evidence that a male classed as a yearling could be adult.

Total body fat was determined by ether extraction of aliquots of oven-dried (95°C) carcasses; lean dry body weight was calculated by subtracting total body fat from the dried carcass weight. Complete details of carcass analysis are given in Ankney and Scott (1980).

RESULTS

The ratio of adult to yearling males in our sample was 1.56:1, which is very similar to the ratio (1.65:1) reported by Darley (1968) from a sample trapped during the breeding season. Birds were collected in breeding habitat (71%) and feeding habitat (29%), but the proportion collected in breeding habitat was independent ($P > 0.5$, G-test) of social group: single—75%, paired—67%, male group—75%, mixed party—69%. Also, 71% of adults and 70% of yearlings were collected in breeding habitat. Thus, the proportions of adults and yearlings we collected from each social group were not biased by where we collected (see Scott and Ankney [1979] for details about habitats). The social group from which a male was collected was not independent ($P < 0.025$) of the male's age (Table 1). Yearlings were more likely to be paired or in male groups and adults were much more likely to be single.

Although there were no significant differences ($P > 0.1$) in mean body weights among social groups, the mean weights of paired males were the

Table 1
Social Group vs Age of Male Brown-headed Cowbirds

	Social group				
	Single	Paired	Male group	Mixed party	Total
Adult	28 (40%)	10 (14%)	11 (16%)	21 (30%)	70
Yearling	7 (16%)	11 (24%)	15 (33%)	12 (27%)	45
		G = 11.164, $P < 0.025$			

heaviest and those of birds from male groups were the lightest (Table 2A). However, when the data for adults and yearlings were combined (they did not differ in body weight [Ankney and Scott 1980]), and paired males tested against all other males, we found that paired males were heavier ($P < 0.05$, Table 2B). This is especially striking as the 'all other male' category undoubtedly contained some paired males. For example, mixed parties frequently are formed when a pair of cowbirds is joined by one or more males and, thus, a male collected from a mixed party could have been the paired male.

There were no significant differences ($0.25 > P > 0.1$) in mean fat reserves or lean dry weights (an index of protein reserves) among males in the four social groups. However, in both cases the mean for paired males was the largest and that for males from male groups was smallest. This suggests that paired males were heaviest because they had slightly larger fat and protein reserves.

Table 2
Body Weight vs Social Group of Male Brown-headed Cowbirds[a]

	Social group				
A. Adults and yearlings	Single $\bar{x} \pm$ SE	Paired $\bar{x} \pm$ SE	Male group $\bar{x} \pm$ SE	Mixed party $\bar{x} \pm$ SE	P[b]
Adult weight (g)	51.7 ± 0.5	52.3 ± 1.0	50.4 ± 0.8	50.8 ± 0.7	$0.25 > P > 0.1$
Yearling weight (g)	50.9 ± 1.4	52.6 ± 0.9	50.3 ± 0.8	51.2 ± 0.8	$0.25 > P > 0.1$

	Social group		
B. Combined data	Paired males $\bar{x} \pm$ SE	All other males $\bar{x} \pm$ SE	P
Male weight (g)	52.5 ± 0.6	51.0 ± 0.3	$0.05 > P > 0.01$

[a] Sample sizes as in Table 1.
[b] Probability, from one-way ANOVA, that means in a row differ by chance.

DISCUSSION AND HYPOTHESIS

Possibly some single males were actually paired; Darley (1968) noted that although a female was normally alone when searching for nests, her mate was usually nearby on a prominent perch or "singing tree." However, such males eventually re-joined the female and if all single males were paired then the age ratio would have been similar in the single and paired categories, but it was not (10:11 vs 28:7 = $P < 0.025$, Table 1).

There is an anomaly in the social biology of male cowbirds: yearlings appear as likely as adults to participate in breeding. That is particularly puzzling because the sex ratio of breeding cowbirds is strongly skewed (1.5:1) in favor of males (Laskey 1950, Darley 1971, Payne 1973). Clearly, under such conditions and strict monogamy, one-third of all males would not obtain mates and it could be expected that yearlings would be excluded from breeding or participate much less than adults, especially as adult males return in spring almost 2 weeks, on average, before yearling males (Darley 1968). Yearling males in several other icterids participate little or not at all in breeding. For instance, adult male Red-winged Blackbirds (*Agelaius phoeniceus*) are much more likely to obtain territories, and thus mates, than are yearlings (Payne 1979), and adults are dominant over yearlings (Searcy 1979). However, all available evidence shows that yearling male cowbirds do breed. First, the yearling and adult testes cycles are very similar (Scott and Middleton 1968); Darley (1968) found that of 19 adult and 16 yearling males collected in late June, the testes of 16 adults and 15 yearlings contained mature sperm (testes of three adults and one yearling were regressed). Second, Darley (1968) showed that in 32 individually marked, mated pairs there were 21 adult and 11 yearling males, which was similar to the overall age ratio of males in that population. Third, Darley (1978) found that under laboratory conditions, yearlings were as equally likely as adults to obtain mates. Finally, and most important, Darley (1968) demonstrated that some adults do not obtain mates. When he removed 15 mated males from the population, 12 were replaced by eight adults and four yearlings; 9 of the 12 were previously unmated and the other three were already mated and became bigamists (Darley did not report the age of the bigamists).

We have developed an hypothesis to explain the foregoing anomaly which also rationalizes the contradictory reports about cowbird mating systems. We propose that the mating system of cowbirds is a combination of monogamy and promiscuity which occurs because males use two tactics to obtain copulations. The first is to obtain a mate, vigorously guard her from other males, and thus monopolize copulations with her (hereafter called 'paired' males). Apparently, larger, more dominant males, are most suc-

cessful at this (Table 2B). Darley (1968) observed that in 18 mated male–unmated male encounters, mated males were dominant in 16 ($P < 0.001$). The second tactic is either to not attempt to pair, or if unsuccessful at pairing, to steal copulations from 'paired' males. Possibly, the second tactic is not really a tactic, in an evolutionary sense, but simply a result of some males being unsuccessful at pairing, and thus having to be 'sneaky' males. In either case, given the skewed sex ratio, there are many males which can only obtain copulations by stealing them from 'paired' males. Darley's (1968) data suggest that at least some 'sneaky' males are successful. He observed seven copulations and in three the male was not the one paired to the copulating female. Elliot (1980) observed copulation by the same male with different females and vice versa, but he did not know which, if any, were 'paired' males.

Do cowbirds actually form pairs? We suggest that from the female's viewpoint they do not. This is logical because of the peculiar breeding biology of cowbirds. There is no parental care by cowbirds and it is the female which defends a territory (Darley 1968). All a female cowbird gets from a male is genetic material, and, through the guarding behavior of the 'paired' male (Laskey 1950, Darley 1968), some relief from harassment by other males, especially when she is feeding. However, the presence of a male may be a cost for the female when she is searching for host nests; a female normally drives away the 'paired' male before searching for nests (Darley 1968). Wittenberger and Tilson (1980:200, Hypothesis 3) noted that for monogamy to evolve it was not necessary for a female to benefit from being guarded by a male, but "the costs of resisting the male's continual presence must exceed the cost of accepting his presence." Apparently, a female cowbird accepts a male's presence when it benefits her and not when there is a cost.

A female cowbird has little or no reason to be faithful to the 'paired' male and may increase her fitness by being receptive to other males. If the 'paired' male is adept at guarding and prevents other males from copulating with her, that is an excellent trait to pass on to her sons. But, if another male is sufficiently sneaky to circumvent the 'paired' male, that ability is also worth passing on. It is difficult to see how a female's fitness could be lowered by mating with a 'sneaky' male; even if the cuckolded 'paired' male were to desert her he would quickly be replaced, as shown by Darley's (1968) removal experiment.

The average female cowbird, in southern Ontario, lays about 40 eggs over 8 weeks (Scott and Ankney 1980) and the average interval between clutches is about 3 days (Scott 1978). During this interval, most females have large ovarian follicles ready to ovulate within a day or so (Scott and Ankney, unpubl.). Thus, most females are continuously susceptible to

fertilization for a long period, thereby greatly increasing the chances of 'sneaky' males to steal copulations. This contrasts markedly with the pattern of fertility in most other birds.

That male cowbirds establish dominance hierarchies and the dominant males become the 'paired' males (Rothstein 1972, Darley 1978) suggests that there is value in being a 'paired' male. Thus, there should be selection for increased body size in male cowbirds. Male cowbirds are about 25% heavier than females (Ankney and Scott 1980), but that is much less than the dimorphism in some other icterids, e.g., Red-winged Blackbirds—65% (Brenner 1968), Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*)—80% (Searcy 1979), in which male dominance is important in mating success. Large adult male cowbirds apparently have higher mortality rates at winter roosts than do smaller adult males (Johnson et al. 1980). However, that cannot counter selection for increased size if only larger, dominant males copulate, especially as there was no relation between body size and mortality rate in juvenile males (Johnson et al. 1980), i.e., differential mortality does not occur until after males have had an opportunity to breed. We hypothesize that the selection for increased size in males is countered because smaller males are able to steal copulations.

Why are adult males single more frequently than are yearlings? This may result from the higher winter mortality of large adults (Johnson et al. 1980 (in winter, adult males include the yearling males from the previous breeding season). Thus, in the breeding season, the yearling cohort may contain as many large males as the adult group, resulting in more adults being unpaired. However, our data show that adults did not weigh less, on average, than yearlings. Possibly, some adults do not attempt to pair and employ a 'sneaky' strategy throughout the breeding season. We cannot explain why that should be a better tactic for adults than for yearlings.

A mating system such as we have proposed could easily lead researchers to conclude differently about the system. Only intensive observations of marked birds (e.g., Darley 1968) would reveal the monogamous aspects of the system, i.e., that a particular female is usually seen with a particular male. More casual observations of marked birds (e.g., Nice 1937, Elliot 1980) or of unmarked birds (Payne 1973) would miss that and thus lead to the conclusion that cowbirds are promiscuous or polygamous. Studies of captive cowbirds would suggest a monogamous system if several males are placed with one female (e.g., Rothstein 1972, Darley 1978) or a polygynous system if several males are placed with several females (West et al. 1981b). Under such conditions the males establish a clear dominance hierarchy and the dominant male can successfully guard the female(s) from subordinate males.

To summarize, we propose that male cowbirds try to pair with females,

but, due to the skewed sex ratio, not all are able to do so. The unpaired males are apparently quite successful at stealing copulations from 'paired' males. It seems likely that 'paired' males also attempt to steal copulations, i.e., they may have a "mixed reproductive strategy" (Trivers 1972), similar to that of Bank Swallows (*Riparia riparia*) (Beecher and Beecher 1979). Females may be quite passive in this system and are as promiscuous as the 'paired' male allows. Such a situation may not be that uncommon in other species (see Bray et al. 1975, Beecher and Beecher 1979, Fujioka and Yamagishi 1981) but is perhaps more pervasive in cowbirds because the greatly extended laying period of females gives 'sneaky' males many opportunities to steal copulations.

More data are needed to evaluate the mating system of cowbirds, e.g., When, where and how frequently do females copulate? Does the social status of a male change in subsequent breeding seasons? Are there differences in annual return rates of banded males from different social groups? Particularly valuable would be information about the frequency at which 'unpaired' males fertilize eggs. Vasectomizing paired males would determine whether or not unpaired males obtain copulations, but not how successful they normally are at obtaining fertilizations. An electrophoretic analysis of the paired male, his female and her offspring would accomplish that (see Sherman 1981).

SUMMARY

The mating system of Brown-headed Cowbirds (*Molothrus ater*) is poorly understood despite frequent comments in the literature. Cowbirds have been reported to be monogamous, polygynous, or promiscuous. We present an hypothesis that the mating system of cowbirds combines monogamy and promiscuity. It is based on our observations of social groupings and weights of wild adult and yearling males, and on published observations of social behavior of cowbirds. We propose that males use two tactics to obtain copulations. The first is to guard a female from other males, i.e., be a 'paired' male to monopolize her copulations. The second is to be a 'sneaky' male and to steal copulations from 'paired' males. 'Paired' males could also be 'sneaky' males. Females are probably as promiscuous as the 'paired' male allows. This system is likely because: (1) the sex ratio of 1.5 males to 1 female excludes many males from being 'paired'; (2) females have no apparent reason to be faithful to the 'paired' male and may increase their fitness by copulating with 'sneaky' males; (3) females are continuously fertile for 8 weeks, thus 'sneaky' males have many opportunities to steal copulations.

ACKNOWLEDGMENTS

We thank S. Johnson, R. Seguin and D. Seip for helping us collect cowbirds and the many landowners who gave us permission to collect cowbirds. P. Handford, J. Millar, S. Rothstein, P. Weatherhead and an anonymous reviewer made helpful suggestions on the manuscript. The research was supported by the National Sciences and Engineering Research Council of Canada.

LITERATURE CITED

ANKNEY, C. D. AND D. M. SCOTT. 1980. Changes in nutrient reserves and diet of breeding Brown-headed Cowbirds. Auk 97:684–696.

BEECHER, M. D. AND I. M. BEECHER. 1979. Sociobiology of Bank Swallows: reproductive strategy of the male. Science 205:1282–1285.

BRAY, O. E., J. KENNELLY, AND J. GUARINS. 1975. Fertility of eggs produced in territories of vasectomized Red-winged Blackbirds. Wilson Bull. 87:187–198.

BRENNER, F. J. 1968. Energy flow in two breeding populations of Red-winged Blackbirds. Am. Midl. Nat. 79:289–310.

DARLEY, J. A. 1968. The social organization of breeding Brown-headed Cowbirds. Ph.D. thesis, Univ. Western Ontario, London, Ontario.

———. 1971. Sex ratio and mortality in the Brown-headed Cowbird. Auk 88:560–566.

———. 1978. Pairing in captive Brown-headed Cowbirds (*Molothrus ater*). Can. J. Zool. 56:2249–2252.

ELLIOT, P. F. 1980. Evolution of promiscuity in the Brown-headed Cowbird. Condor 82: 138–141.

FRIEDMANN, H. 1929. The cowbirds, a study of the biology of social parasitism. Charles C. Thomas, Springfield, Illinois.

FUJIOKA, M. AND S. YAMAGISHI. 1981. Extramarital and pair copulations in the Cattle Egret. Auk 98:134–144.

JOHNSON, D. M., G. L. STEWART, M. CORLEY, R. GHRIST, J. HAGNER, A. KETTERER, B. MCDONNELL, W. NEWSOM, E. OWEN, AND P. SAMUELS. 1980. Brown-headed Cowbird (*Molothrus ater*) mortality in an urban winter roost. Auk 97:299–320.

LASKEY, A. R. 1950. Cowbird behavior. Wilson Bull. 62:157–174.

NICE, M. M. 1937. Studies in the life history of the Song Sparrow. I. Trans. Linn. Soc. 4.

PAYNE, R. B. 1973. The breeding season of a parasitic bird, the Brown-headed Cowbird in central California. Condor 75:80–99.

———. 1979. Sexual selection and intersexual differences in variance of breeding success. Am. Nat. 114:447–452.

ROTHSTEIN, S. I. 1972. Territoriality and mating system in the parasitic Brown-headed Cowbird (*Molothrus ater*) as determined from captive birds. Am. Zool. 12:77.

———, J. VERNER, AND E. STEVENS. 1980. Range expansion and diurnal changes in dispersion of the Brown-headed Cowbird in the Sierra Nevada. Auk 97:253–267.

SCOTT, D. M. 1978. Using sizes of unovulated follicles to estimate the laying rate of the Brown-headed Cowbird. Can. J. Zool. 56:2230–2234.

——— AND A. L. A. MIDDLETON. 1968. The annual testicular cycle of the Brown-headed Cowbird (*Molothrus ater*). Can. J. Zool. 46:77–87.

——— AND C. D. ANKNEY. 1979. Evaluation of a method for estimating the laying rate of Brown-headed Cowbirds. Auk 96:483–488.

——— AND ———. 1980. Fecundity of the Brown-headed Cowbird in southern Ontario. Auk 97:677–683.

SEARCY, W. A. 1979. Size and mortality in male Yellow-headed Blackbirds. Condor 81: 304–305.

SELANDER, R. K. AND D. R. GILLER. 1960. First-year plumage of the Brown-headed Cowbird and Red-winged Blackbird. Condor 62:202–214.

SHERMAN, P. W. 1981. Electrophoresis and avian genealogical analyses. Auk 98:419–422.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 136–179 *in* Sexual selection and the descent of man 1871–1971 (B. Campbell, ed.). Aldine-Atherton, Chicago, Illinois.

WEST, M. J., A. P. KING, AND D. H. EASTGER. 1981a. The cowbird: reflections on development from an unlikely source. Am. Sci. 69:56–66.

———, ———, AND ———. 1981b. Validating the female bioassay of cowbird song: relating differences in song potency to mating success. Anim. Behav. 29:490–501.

WITTENBERGER, J. F. AND R. L. TILSON. 1980. The evolution of monogamy: hypotheses and evidence. Ann. Rev. Ecol. Syst. 11:197–232.

DEPT. ZOOLOGY, UNIV. WESTERN ONTARIO, LONDON, ONTARIO N6A 5B7, CANADA. ACCEPTED 10 MAR. 1982.

Wilson Bull., 94(3), 1982, pp. 269–281

KLEPTOPARASITISM BY SOUTH POLAR SKUAS ON BLUE-EYED SHAGS IN ANTARCTICA

Stephen J. Maxson and Neil P. Bernstein

Kleptoparasitism, or piracy, is widespread among the Laridae and Stercorariidae (see Brockmann and Barnard 1979, for review). While several studies have quantified the parasitism of Great Skuas (*Catharacta skua*) on a number of North Atlantic seabirds (Meinertzhagen 1959, Andersson 1976, Furness 1978, Arnason and Grant 1978), only anecdotal accounts have treated the subject for Chilean Skuas (*C. chilensis*) and South Polar Skuas (*C. maccormicki*) (Murphy 1936, Holdgate 1963, Burton 1968, Watson 1975).

We casually observed 50–100 chases of Blue-eyed Shags (*Phalacrocorax atriceps*) by South Polar Skuas at Palmer Station, Antarctica from mid-December 1978 to early February 1979. Although some chases involved physical attacks on flying shags, only once did a shag regurgitate food. Since chases often covered distances of 500 m or more, this seemed an energetically expensive foraging technique so we investigated it in detail during austral summer 1979–80. Our objectives were: (1) to determine methods of attack by skuas and response to attack by shags; (2) to determine whether chases were more frequent near to (<1 km) or away from (3.5–7 km) the shag colony; (3) to determine whether environmental factors contributed to the number and success of chases; (4) to estimate whether kleptoparasitism is energetically profitable for skuas; and (5) to compare chase success of South Polar Skuas with that of other skuas, jaegers (*Stercorarius* spp.) and gulls (*Larus* spp.) which pirate food by means of aerial pursuits.

STUDY AREA AND METHODS

The study was conducted from 28 October 1979–11 March 1980, in the vicinity of Palmer Station, Anvers Island (64°46′S, 64°03′W) near the Antarctic Peninsula (Fig. 1). During our study pack-ice cover of the ocean (Fig. 1) varied from 0–100%, changing daily depending on wind direction and velocity, and tidal currents.

A variety of seabirds nest on exposed peninsulas projecting from glacier-covered Anvers Island and on equally exposed small rocky islands nearby (Parmelee et al. 1977). Breeding Brown Skuas (*C. lonnbergi*) were outnumbered by breeding South Polar Skuas approximately 25:1 but typically held territories near Adélie Penguin (*Pygoscelis adeliae*) colonies from which they excluded the smaller south polars. South Polar Skuas nested on virtually all islands and ice-free peninsulas near Palmer Station (Fig. 1), and a minimum of 241 pairs successfully hatched chicks during 1979–80. An undetermined number of nonbreeders and/or failed breeders were also present and gathered in groups of up to 90 at a glacial melt pond near the base of Norsel Point and on Christine Island. The only Blue-eyed Shag colony within

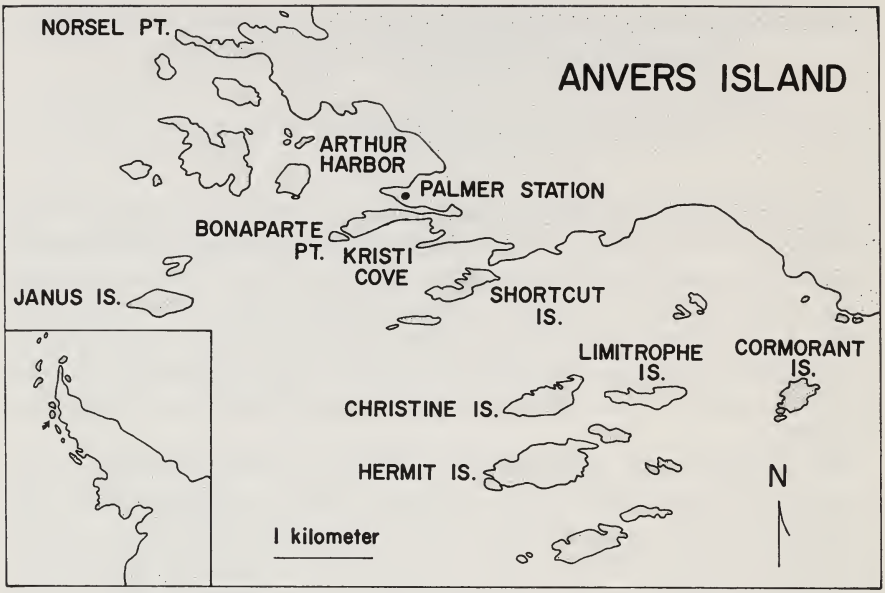


FIG. 1. Palmer Station, Antarctica and vicinity. (Arrow in inset indicates location of Anvers Island relative to the Antarctic Peninsula.)

15 km of Palmer Station is on Cormorant Island where nest counts totaled 485 (31 December 1978) and 326 (19 December 1979).

Scheduled observations were carried out from two locations—atop the shag colony on Cormorant Island facing northwest and near the base of Bonaparte Point (4 km from the colony) facing southwest. Each site afforded approximately a 1 km^2 view of an area through which shags frequently travelled.

During observation periods lasting 3–24 h, we recorded weather and pack ice conditions, the number of shags flying toward the colony, the number of shags flying away from the colony, the number of chases by skuas, the number of skuas involved in chases, attack methods of skuas, response to attack by shags, and the number of regurgitations by shags. We also recorded all other chases of shags whenever observed.

RESULTS

Breeding phenology.—Blue-eyed Shags are present in the Palmer area year round and often remain at the breeding colony during the winter (Holdgate 1963; Glass 1978; Bernstein and Maxson, unpubl.). During the 1979–80 season, courtship, pairing and nest-building began in September; egg-laying occurred early November to mid-December; hatching began in early December; and chicks were attended and fed by both parents from hatch to March. Time budget data indicate that each parent foraged once per day while the other remained at the nest. As chicks neared fledging in mid-February, both parents often foraged simultaneously.

South Polar Skuas returned to the study area in mid-November. Egg-laying ranged from mid-January through mid-February. When we departed the study area on 11 March, a few older chicks were fledging but many others were still in the downy stage (Pietz and Maxson, unpubl.).

Qualitative aspects of chases.—A common flight path for shags returning to the colony was south across Arthur Harbor, over or around Bonaparte Point, southwest across Kristi Cove and through the narrow gap between Shortcut and Anvers islands (see Fig. 1). Sixteen and 19 pairs of South Polar Skuas nested on Bonaparte Point and Shortcut Island, respectively, making Kristi Cove an area of potentially numerous skua-shag interactions.

Shags approached Cormorant Island from all directions but most often from the west or northwest. Six pairs of South Polar Skuas occupied breeding territories on Cormorant Island during 1979–80, although only two of these produced eggs. A total of 107 pairs of skuas bred on nearby Limitrophe, Christine, and Hermit islands from where they could readily harass shags flying to and from the colony.

Skuas attempted to induce shags to regurgitate by aerial harassment. Being faster, more aerobatic flyers, skuas readily overtook and outmaneuvered shags in most situations. Sometimes skuas simply flew close behind a shag or swooped at it, but often they attacked the shag by biting at its back, rear, or belly. If a shag regurgitated, the skua caught the fish in mid-air or retrieved it from the water.

Shags responded to chases in several ways. Single shags or small groups often swerved away from an approaching skua in turns of up to 180°. This maneuver was sometimes successful in ending a chase. Larger groups of shags (10–20) rarely turned away and remained in formation until attack was imminent. Then the flock typically split into smaller units flying different directions whereupon the skua focused on one group or an individual and continued the chase. If the flock was large (>30), attack by a single skua did not result in fragmentation of the flock but merely perturbations in the immediate vicinity of the attacker.

The most effective evasive action by shags was landing on the water, though they did not actually land until skuas struck them or were about to strike. Occasionally a skua attempted to prevent its victim from landing by flying beneath it and biting at its belly even when the shag was only 2 m above the surface, but a shag in this position was still able to land if open water was available.

If shags reached the water without regurgitating, skuas often gave up. Persistent skuas, however, swooped at the shag. Shags responded by either jumping up and biting at the skua or by diving. In the latter case, the skua either flew off, hovered overhead, or landed on an ice floe until the shag

Table 1
Summary of Scheduled Observations at Shag Colony and at Kristi Cove 4 km from Colony

Observation site	No. h	Shags flying toward colony			
		No. shags	No. chases	% chased	No. regurg.
Cormorant Island	72	1684	4	0.2	0
Kristi Cove	93	726	71	9.8	2

	Shags flying away from colony				
	No. shags	No. chases	% chased	No. regurg.	Chases per h
Cormorant Island	1384	1	0.1	0	0.1
Kristi Cove	895	21	2.3	0	1.0

surfaced, whereupon the skua swooped again. This tactic was never observed to be successful, although Murphy (1936) did observe skuas snatching fish from shags as they surfaced from a foraging dive.

Quantitative aspects of chases.—Scheduled observations totaled 165 h (Table 1). Although more shags were observed near the colony than at Kristi Cove, they were attacked less often ($\chi^2 = 159.2$, df = 1, $P < 0.001$). At Kristi Cove shags were chased more often when flying toward than when flying away from the colony ($\chi^2 = 41.3$, df = 1, $P < 0.001$).

During scheduled observations, no shags within 1 km of the colony (Table 1) were induced to regurgitate fish. Two birds arriving with nest material (aquatic vegetation) dropped the vegetation when chased, but the skuas made no attempt to retrieve these items. At Kristi Cove no pursuits of shags flying away from the colony were successful and only two (2.5%) chases of shags flying toward the colony resulted in regurgitation.

Overall, we observed 280 chases of which 13 (4.6%) resulted in regurgitation (Table 2). Although time spent at Cormorant Island was roughly equivalent to time in the field at other locations and despite nearly equal chase success rates near and away from the colony, only 27 (9.6%) chases were witnessed at the colony. The majority (73%) of pursuits (and all successful chases) were of shags flying toward the colony. Skuas were unsuccessful when chasing shags flying away from the colony or when swooping at swimming shags.

To investigate factors that potentially influence chase success we categorized chases (3.5–7 km from the colony) relative to the numbers of shags and skuas involved (Table 3). Success rate for single skuas chasing lone shags was 4.6%, and no increase in success was evident when several

TABLE 2
CHASE SUCCESS RELATIVE TO SHAG BEHAVIOR AND CHASE LOCATION

	3.5–7 km from colony			<1 km from colony		
	No. chases	Successful		No. chases	Successful	
		No.	%		No.	%
Shags flying away from colony	47	0	0.0	6	0	0.0
Shags flying toward colony	188	12	6.4	16	1	6.2
Shags swimming	18	0	0.0	5	0	0.0
Total	253	12	4.7	27	1	3.7

skuas pursued a single shag or when one skua pursued a group of shags. We observed groups of two to ten skuas ($\bar{x} = 3.9 \pm 3.1$) pursuing groups of shags. These multiple pursuits resulted in a four-fold increase (to 21%) in the probability that at least one shag would regurgitate. However, skuas in these groups were clearly acting as individuals and when the flocks split up, each typically pursued a different shag. When success rate per skua was calculated for these groups there was no increase in success.

In 68 chases where skuas did not strike any of the birds pursued, only 5 of 227 shags (2.2%) regurgitated, but in 32 of these chases skuas gave up before closing within striking distance. Of 64 chases where skuas struck shags, eight (12.5%) resulted in regurgitations (Table 4). Most often skuas flew immediately behind shags and bit at their tail area. The data suggest, however, that greater success was achieved when a skua flew beneath a shag and bit upwards at the shag's belly.

Influence of environmental factors.—Although our study spanned 136 days, 12 of the 13 observed regurgitations occurred between 13–15 December. At 17:00, 13 December, we noted an unusual number of chases. From atop one of the Palmer Station buildings we observed the Arthur Harbor and Kristi Cove areas (approx. 2 km^2) until 18:45, recording 38 chases with

TABLE 3
CHASE SUCCESS RELATIVE TO NUMBER OF SKUAS AND SHAGS INVOLVED

No. shags	No. skuas	No. chases	No. regurgitations	% success/ chase	% success/ skua
1	1	43	2	4.6	4.6
1	>1	7	0	0.0	0.0
>1	1	36	2	5.5	5.5
>1	>1	38	8	21.0	5.3

TABLE 4
SUMMARY OF CHASES WHERE SKUA STRUCK SHAG

Where struck	No.	No. regurgitations	% success
Rear	37	4	10.8
Back	6	0	0.0
Belly	15	4	26.7
Back and belly	6	0	0.0
Total	64	8	12.5

eight regurgitations. The chase rate of 22/h was much greater than that observed during any of the scheduled watches (Table 1). All five instances of shags regurgitating without first being struck occurred during this 1.7-h period. Most regurgitated as the skua approached closely and appeared about to strike but one bird regurgitated to a skua which was flying well below it and still about 20 m away.

The environmental factor common to all instances of successful chases (including the one observed during the 1978–79 season) was the presence of dense pack ice, which influenced the number and success rate of chases in two ways. First, shags were more vulnerable at this time because lack of open water areas precluded their most effective means of escape (shags are not maneuverable fliers and have difficulty landing in small patches of open water between ice floes, particularly when their flight is being disrupted by a skua). When unable to find a suitable landing site, the surest way for a shag to rid itself of a pursuing skua was to regurgitate a fish. Second, South Polar Skuas near Palmer Station were primarily dependent on the sea for food since Brown Skuas controlled penguin colonies and edible garbage from the station was sealed in metal barrels. Consequently, when dense pack ice stretched to the horizon (a situation not uncommon during the breeding season [Parmelee et al. 1978]) skuas had to fly long distances to find open water areas where they could capture fish or krill. As an alternative, they could remain near their territories and increase their efforts to steal food from shags.

Support for these hypotheses is presented in Table 5. On 8 December the pack ice was 1–2 km away from the shore of Anvers Island leaving large areas of ice-free water. In contrast, the pack ice on 14 December covered over 95% of the area extending from the shore of Anvers Island to the horizon. Although many shags flew across Kristi Cove on both days, significantly more chases occurred ($\chi^2 = 43.4$, df = 1, $P < 0.001$) when the pack ice was in. The same pattern is indicated by increases in the

TABLE 5

INFLUENCE OF PACK ICE ON CHASE FREQUENCY AND SUCCESS DURING TWO 24-H SCHEDULED OBSERVATIONS AT KRISTI COVE

Date	Pack ice	No. shags	No. chases	% chased	No. regurgitations	Chases/h
8 Dec.	Out	681	9	1.3	0	0.4
14 Dec.	In	661	62	9.4	2	2.6

percentage of shags chased and in the number of chases per hour from 8–14 December.

Further evidence is that all pack ice blew out to sea during a storm on 9–10 January 1980, leaving the Palmer Station area largely ice free through the end of the breeding season. Only 8 (none successful) of 280 total chases observed occurred after 9 January, although food demands for both skuas and shags peaked after that date due to food requirements of chicks.

DISCUSSION

Factors influencing chase success.—An obvious influence on chase success is whether a shag is carrying food. A bird leaving the colony to forage probably has little or no food in its stomach and no chases of shags flying away from the colony were successful (Tables 1, 2). Likewise, a bird returning to the colony after foraging has a high probability of carrying food. Successful kleptoparasites would be expected to discriminate between the two groups. This appears to be the case, as 73% of chases (Table 2) as well as the higher proportion of shags chased (Table 1) were birds flying toward the colony. Cues skuas used to distinguish the two groups (even at distances of 7 km from the colony) remain unknown as there were no visual differences in flight speed or body contour apparent to us. Perhaps skuas have learned to associate food with the shags' flight direction simply through trial and error chases of both groups.

Increasing the number of pursuers usually increases chase success while decreasing individual success (Hatch 1970, 1975; Grant 1971; Andersson 1976; Hulsman 1976; Verbeek 1977; Arnason and Grant 1978; Taylor 1979). In the present study, chase success increased from about 5% when single skuas chased either individuals or groups of shags to 21% when groups of skuas chased groups of shags (Table 3). Success per individual, however, remained near 5%. Whereas other workers typically report multiple chases of individuals, we most often observed multiple chases of groups which became several individual chases after shag flocks divided.

Andersson (1976) reported that pursued Northern Gannets (*Sula bas-*

sana) were no more likely to regurgitate when struck by Great Skuas than when untouched. In contrast, we found that 8 of 64 (12.5%) shags struck during chases regurgitated (Table 4), whereas only 5 of 227 (2.2%) shags not struck did so.

Dense pack ice influenced the number of chases by making the skuas' primary food (fish and krill) more difficult to obtain and influenced chase success by making it difficult for shags to escape skuas by landing on the water. All observed regurgitations occurred under these conditions. Similarly, at a colony where Common Puffins (*Fratercula arctica*) had to fly 1 km over land before reaching the nesting cliffs and could not readily escape to the sea, Parasitic Jaegers (*Stercorarius parasiticus*) achieved high chase success (51–69%) (Grant 1971, Arnason and Grant 1978) compared with success rates (15–22%) at colonies adjacent to the sea (Andersson 1976; Furness 1977, 1978).

Comparison with other kleptoparasites.—The Appendix compares chase success of South Polar Skuas with that of other skuas, jaegers, and gulls which engage in aerial pursuits of hosts. With the exception of two cases with 0% success (Furness 1977), which can be discounted due to very small sample sizes, the overall chase success of the present study is the lowest reported for this type of kleptoparasitism. All birds (except Herring Gulls [*Larus argentatus*] [Verbeek 1977]) achieving a success rate under 15% parasitized additional species at the same site which yielded higher success. At Palmer Station, Antarctic Terns (*Sterna vittata*), Southern Black-backed Gulls (*L. dominicanus*) and Southern Giant Fulmars (*Macronectes giganteus*) also bred and were potential hosts. In two seasons, however, we observed fewer than 10 chases of either terns or gulls and no chases of Giant Fulmars. Holdgate (1963) likewise reported that skuas confined most parasitic chases to shags in the Palmer Station area.

Profitability of kleptoparasitism to skuas.—In view of the low chase success observed, it is of interest to determine whether skuas achieve an energy profit through kleptoparasitism. While precise calculations are beyond the scope of this study, some energy cost/benefit approximations can be made. The mass-specific oxygen consumption of nine South Polar Skuas at Palmer Station was found to be 1.30 l O_2/kg/h ± 0.05 (R. Ricklefs, pers. comm.), a value nearly double that predicted by the equation of Lasiewski and Dawson (1967). Weights of 80 South Polar Skuas captured near the station averaged 1156 ± 98 g (Pietz and Maxson, unpubl.). Using these values the standard metabolic rate (SMR) of an average-weight skua is 29.6 kJ/h. At an average chase success of 4.6% (Table 2), a skua would require over 20 chases before causing a shag to regurgitate. Chases of 500 m were common and some continued for 1 km or more. Thus, to obtain one fish, a skua would likely have to fly a total of 10–20 km at top speed

chasing shags, plus, perhaps a similar distance at energetically less costly flight while returning to its territory. Flight speed of Blue-eyed Shags was approximately 48 kmph (Bernstein and Maxson, unpubl.). If, for example, a skua flew 15 km at chase speeds of 60 kmph and returned at 40 kmph, and if chasing and returning cost 15.2 × SMR (King 1974) and 8 × SMR, respectively, the bird would expend roughly 201.3 kJ obtaining a fish.

Fish regurgitated to skuas were ca. 9–14 cm long. A fish of similar size (13.6 cm) regurgitated at the colony during shag banding operations weighed 40 g. Assuming that energy content of fish equals 1.14 Kcal/g (4.77 kJ/g) fresh weight (Dunn 1975) and that skuas have a digestive efficiency of 80% (Uramoto 1961, Kahl 1964, Dunn 1975, Kushlan 1977, Cooper 1978), a skua pirating a similar fish would obtain 152.6 kJ of metabolizeable energy. In the example above, the bird would suffer a net energy loss of 48.7 kJ. Clearly, variation in the above factors will alter the cost/benefit ratio, but these calculations suggest that it would be difficult for a skua to achieve any substantial energy profit at the low chase success rates observed.

No South Polar Skuas were known to rely on piracy as a major source of food during our study. For example, on 13 days between 8 December 1979–9 March 1980 P. Pietz and G. Maxson (unpubl.) conducted 265 h of scheduled observations on Bonaparte Point in which four pairs of color banded skuas were simultaneously observed for periods of 14–24 h. Only 14 chases (involving both sexes, none successful) by these banded skuas were observed and no individual was seen chasing shags more than three times in a single day. Probably other foods could predictably be obtained, at less expense, under most conditions.

We hypothesize that individual skuas chase shags, in part, to assess their vulnerability to kleptoparasitism. Skuas are opportunistic foragers, clearly aware of the activities of other skuas, and are quickly attracted to the discovery of an ephemeral food source. Regurgitation by shags and the subsequent retrieval of the fish by skuas are conspicuous activities. When shags prove vulnerable, chasing is likely to become contagious and could readily develop into the situation observed on 13 December. Thus, individual skuas would spend relatively little time or energy chasing under most circumstances but would increase their efforts when chasing proved energetically profitable.

SUMMARY

South Polar Skua (*Catharacta maccormicki*) kleptoparasitism on Blue-eyed Shags (*Phalacrocorax atriceps*) was studied at Palmer Station, Antarctica (64°46′S, 64°03′W) from 28 October 1979–11 March 1980. Skuas attempted to induce shags to regurgitate fish by means of aerial harassment. The shags' most effective means of escaping attack was landing on the water. Of 280 chases observed, only 13 (4.6%) were successful. This success rate is lower than that reported for other skuas, jaegers and gulls which pirate food through aerial pursuits

of hosts. The majority of chases (73%) were of shags returning to their breeding colony, but most chasing occurred away from (3.5–7 km) the colony itself. Chase success increased to 21% when groups of skuas pursued groups of shags but success per skua remained near 5%. Skuas struck shags during 64 chases resulting in 8 (12.5%) regurgitations. In contrast, during 68 chases where no shags were struck, only 5 of 227 shags (2.2%) regurgitated. All successful chases occurred during periods of dense pack ice which left few areas of open water. Dense pack ice caused an increase in chasing because it made the skuas' primary food (fish and krill) more difficult to obtain. Lack of open water also increased chase success by making it more difficult for shags to find suitable landing sites to escape attack. Energy budget estimates suggest it is unlikely that skuas achieve an energy profit at the low success rates observed and no skuas were known to rely on piracy as a major food source during the study.

ACKNOWLEDGMENTS

This study was supported by NSF grant DPP77-22096 to D. Parmelee. We are grateful for the logistic support provided by the Holmes and Narver personnel at Palmer Station. P. Pietz and G. Maxson helped with data collection and generously allowed us access to unpublished data on skua breeding ecology. R. Ricklefs allowed us to cite unpublished data on skua metabolic rates. D. Berube and B. Medvecky assisted with typing and graphics. D. Parmelee, G. Maxson and D. Ainley made helpful comments on the manuscript.

LITERATURE CITED

Andersson, M. 1976. Predation and kleptoparasitism by skuas in a Shetland seabird colony. Ibis 118:208–217.

Arnason, E. and P. R. Grant. 1978. The significance of kleptoparasitism during the breeding season in a colony of Arctic Skuas *Stercorarius parasiticus* in Iceland. Ibis 120:38–54.

Behn, F., J. D. Goodall, A. W. Johnson, and R. A. Phillippi B. 1955. The geographical distribution of the Blue-eyed Shags, *Phalacrocorax albiventer* and *Phalacrocorax atriceps*. Auk 72:6–13.

Brockmann, H. J. and C. J. Barnard. 1979. Kleptoparasitism in birds. Anim. Behav. 27:487–514.

Burton, R. W. 1968. Breeding biology of the Brown Skua, *Catharacta skua lonnbergi* (Mathews), at Signy Island, South Orkney Islands. Br. Antarct. Surv. Bull. 15:9–28.

———. 1970. Biology of the Great Skua. Pp. 561–567 *in* Antarctic Ecology Vol. I. (M. W. Holdgate, ed.). Nature Conservancy, London, England.

Cooper, J. 1978. Energetic requirements for growth and maintenance of the Cape Gannet (Aves: Sulidae). Zool. Afr. 13:305–317.

Corkhill, P. 1973. Food and feeding ecology of puffins. Bird Study 20:207–220.

Dunn, E. K. 1975. Caloric intake of nestling Double-crested Cormorants. Auk 92:553–565.

Furness, R. W. 1977. Effects of Great Skuas on Arctic Skuas in Shetland. Br. Birds 70: 96–107.

———. 1978. Kleptoparasitism by Great Skuas (*Catharacta skua* Brunn.) and Arctic Skuas (*Stercorarius parasiticus* L.) at a Shetland seabird colony. Anim. Behav. 26:1167–1177.

Glass, B. M. 1978. Winter observations of birds at Palmer Station in 1977. Antarct. J. U.S. 13:145.

Grant, P. R. 1971. Interactive behaviour of puffins (*Fratercula arctica* L.) and skuas (*Stercorarius parasiticus* L.). Behaviour 40:263–281.

Hatch, J. J. 1970. Predation and piracy by gulls at a ternery in Maine. Auk 87:244–254.

———. 1975. Piracy by Laughing Gulls *Larus articilla*: an example of the selfish group. Ibis 117:357–365.

Holdgate, M. W. 1963. Observations of birds and seals at Anvers Island, Palmer Archipelago, in 1955–57. Br. Antarct. Surv. Bull. 2:45–51.

Hulsman, K. 1976. The robbing behaviour of terns and gulls. Emu 76:143–149.

Kahl, M. P. 1964. Food ecology of the Wood Stork (*Mycteria americana*) in Florida. Ecol. Monogr. 34:97–117.

King, J. R. 1974. Seasonal allocation of time and energy resources in birds. Pp. 4–70 *in* Avian Energetics (R. A. Paynter, Jr., ed.). Nuttall Ornithol. Club Publ. No. 15.

Kushlan, J. A. 1977. Population energetics of the American White Ibis. Auk 94:114–122.

Lasiewski, R. C. and W. R. Dawson. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. Condor 69:13–23.

Meinertzhagen, R. 1959. Pirates and predators. Oliver and Boyd, London, England.

Murphy, R. C. 1936. Oceanic birds of South America. Am. Mus. Nat. Hist., New York, New York.

Parmelee, D. F., W. R. Fraser, and D. R. Neilson. 1977. Birds of the Palmer Station area. Antarct. J. U.S. 12:14–21.

———, N. Bernstein, and D. R. Neilson. 1978. Impact of unfavorable ice conditions on bird productivity at Palmer Station during the 1977–78 field season. Antarct. J. U.S. 13:146.

Taylor, I. R. 1979. The kleptoparasitic behaviour of the Arctic Skua *Stercorarius parasiticus* with three species of tern. Ibis 121:274–282.

Uramoto, M. 1961. Ecological study of the bird community of the broad-leaved deciduous forest of central Japan. Misc. Rept. Yamashina Inst. Orn. Zool. 3:1–32.

Verbeek, N. A. M. 1977. Interactions between Herring and Lesser Black-backed Gulls feeding on refuse. Auk 94:726–735.

Watson, G. E. 1975. Birds of the Antarctic and Sub-Antarctic. American Geophysical Union, Washington, D.C.

FIELD BIOLOGY PROGRAM, J.F.B. MUSEUM OF NATURAL HISTORY, UNIV. MINNESOTA, MINNEAPOLIS, MINNESOTA 55455. (PRESENT ADDRESS SJM: MINNESOTA DEPT. NATURAL RESOURCES, WETLAND WILDLIFE RESEARCH GROUP, 102 23RD ST., BEMIDJI, MINNESOTA 56601.) ACCEPTED 20 NOV. 1981.

Appendix

Chase Success by Skuas, Jaegers and Gulls Engaging in Aerial Pursuits of Hosts

Kleptoparasite	Host	No. chases	% successful	Source
South Polar Skua	Blue-eyed Shag	280	4.6	This study
Great Skua	Northern Gannet	11	100.0	Meinertzhagen 1959
		93	11.8	Andersson 1976
		69	30.4	Furness 1978
	Common Puffin	32	18.7	Andersson 1976
		233	37.7	Furness 1978
		32	34.4	Arnason and Grant 1978
	Black-legged Kittiwake (*Rissa tridactyla*)	13	15.4	Furness 1978
	Razorbill (*Alca torda*)	38	18.4	Furness 1978
	Common Murre (*Uria aalge*)	113	29.2	Furness 1978
Parasitic Jaeger	Common Puffin	88	21.6	Andersson 1976
		140	50.7	Grant 1971
		1101	68.8	Arnason and Grant 1978
		110	20.9	Furness 1978
		13	15.4	Furness 1977
	Arctic Tern (*Sterna paradisaea*)	87	43.7	Furness 1978
		220	47.7	Furness 1977
		70	40.0[a]	Taylor 1979
	Black-legged Kittiwake	33	33.3	Furness 1978
		16	25.0	Furness 1977
	Razorbill	18	11.1	Furness 1978
		3	0.0	Furness 1977
	Common Murre	27	11.1	Furness 1978
		3	0.0	Furness 1977
Parasitic Jaeger	Sandwich Tern (*Sterna sandvicensis*)	254	23.2[a]	Taylor 1979
	Common Tern (*S. hirundo*)	100	9.0[a]	Taylor 1979
Lesser Black-backed Gull (*Larus fuscus*)	Herring Gull	118	43.2	Verbeek 1977
	Lesser Black-backed Gull	86	20.9	Verbeek 1977

Appendix
Continued

Kleptoparasite	Host	No. chases	% successful	Source
Herring Gull	Herring Gull	10	10.0	Verbeek 1977
	Lesser Black-backed Gull	19	10.5	Verbeek 1977
Herring Gull–Lesser Black-backed Gull	Common Puffin	29	34.5	Arnason and Grant 1978
		15	26.6	Corkhill 1973
Black-legged Kittiwake	Common Puffin	7	42.9	Arnason and Grant 1978
Laughing Gull (*L. atricilla*)	Arctic Tern–Common Tern	87	78.2	Hatch 1970
Silver Gull (*L. novaehollandiae*)	Crested Tern (*S. bergii*)	711	16.7[a]	Hulsman 1976
	Lesser Crested Tern (*S. bengalensis*)	77	6.5	Hulsman 1976

[a] Original data recalculated to fit Appendix.

Wilson Bull., 94(3), 1982, pp. 282–288

INTRASPECIFIC FOOD ROBBING IN GLAUCOUS-WINGED GULLS

Elizabeth Drexler Rockwell

Inter- and intraspecific food robbing, sometimes called kleptoparasitism or piracy, is common in birds, particularly, Falconiformes and Charadriiformes. A critical review of the literature by Brockmann and Barnard (1979) revealed principally descriptions of the behavior without explanations for functional significance. Findings from my investigation of intraspecific food robbing in Glaucous-winged Gulls (*Larus glaucescens*) are provided in response to recommendations by these authors for studies of costs and benefits of food robbing.

PRELIMINARY OBSERVATIONS AND METHODS

During informal visits to Lopez Island, Washington, between 1975 and 1977, I observed intraspecific food robbing in Glaucous-winged Gulls foraging on tidal mudflats at Mud Bay and MacKaye Harbor. During ebb, low and flood tides, gulls plunge-dived in shallow water, searched among seaweed and probed the mud with their bills. They captured clams, crabs, marine worms and organisms too small to be identified by observation. Gulls seized clams with the bill and flew to shore (drop flight) where they dropped the mollusks over firm ground (drop site) from a height of 3–8 m. Clam shells cracked upon impact and gulls descended to pick the meat from the fragments. Gulls cracked exoskeletons of crabs, too large to be swallowed whole, with forceful stabbing of their bills. All other prey was swallowed with one or two gulps without processing.

Three age classes of Glaucous-winged Gulls were recognized on the basis of plumage differences (Robbins et al. 1966). First-year birds were identified by uniform mottled-brown plumage; incomplete white body plumage and mottled-brown mantles with gray patches differentiated second- and third-year birds from adults which were characterized by uniform white body plumage and gray mantles. Robberies were committed within and among age classes. On the mudflats, gulls robbed by supplanting conspecifics dissecting crabs or by seizing clams from the bills of victims. On shore, gulls robbed at drop sites. As soon as conspecifics released clams to crack their shells, robbers dashed to the sites of impact and grasped the mollusks. In the air, victims surrendered prey to robbers during aerial chases. Robbers initiated such chases while victims were flying to drop sites on shore. Robbers retrieved surrendered prey from the ground or caught it on the wing.

These observations suggested that food robbing was profitable if caloric gains per unit time were greater for robbers than for individuals that did not rob. Because it was principally clams that were obtained by robbing, I confined my estimates of cost-benefit ratios to expenditures for handling clams and robbing and caloric gains from the meat of clams. The estimates did not include calculations for other expenditures related to foraging. Nevertheless, they revealed whether robbers acquired more calories for such expenditures as, for example, search of prey, metabolic regulations, growth, and reproduction, than individuals that did not rob. This assumption was made because with few exceptions robbers foraged intensively and robbed only when handling of prey rendered nearby conspecifics vulnerable.

From 5 May–15 July 1978 I observed Glaucous-winged Gulls on tidal mudflats at Mud Bay

and MacKaye Harbor, Lopez Island, Washington. Daily observation periods alternated between the two sites and were conducted from shore, usually with binoculars. Every 60 min, I counted the number of gulls engaged in foraging, feeding and processing food. I recorded the number of captured clams and robbery attempts as well as the types of robberies, types of booty, age classes of robbers and victims, and outcomes of both ground and aerial robberies on an hourly basis. Drop flights commencing with lift off upon capture of clams and terminating with releases of clams over drop sites were timed with a stop watch. Aerial chases commencing with the pursuit of the victims by the robbers and terminating with surrender of prey by the victims or abandonment of the chases by the robbers were also timed with a stop watch. Energy expended on drop flights and aerial chases was estimated with the equation kcal/h = 45.4 $W^{0.73}$ (Hart and Berger 1972) where W is the average weight of Glaucous-winged Gulls, i.e., 1.051 kg (Vermeer 1963). Energy expenditures for ground robberies were assumed to require about 0.01 kcal/robbery because at most they involved a dash over 2–5 m to snatch booty. Methods to estimate energy expenditure for such locomotion are not available (King 1974).

Sizes of captured and robbed clams were estimated. A sample of clams comparable in size and species to captured and robbed clams was collected. The widths of clams were measured and the caloric contents of clams estimated from the weights and calorie charts (U.S. Dept. Agriculture 1973). Focal animal sampling (Altmann 1974) was conducted to observe the behavior of foraging gulls and their interactions with one another. Intervals between consecutive captures of clams by gulls of different age classes were timed with a stop watch.

Captured and stolen clams were identified as sources of caloric gains for robbers. Energy expended for flights to shore to crack clams, dashes over the ground to snatch booty from victims in ground robberies and aerial chases in aerial robberies were identified as caloric expenditures. Robbery attempts were successful if they terminated in favor of the robbers. Caloric expenditure for locomotion on the ground in successful ground robberies and for aerial chases in successful aerial robberies was subtracted from the caloric content of the robbed clam and the difference was identified as a caloric gain. Caloric expenditure for unsuccessful robberies was identified as a caloric loss. Because the identities of gulls were unknown, the number of robbers/h among the foraging gulls was assumed to equal the number of robbery attempts/h.

Average hourly caloric gains and losses were calculated in kcal/robber/h for each age class of robbers at each study site (Table 1). Losses were then subtracted from gains. The difference was compared with a conjectural caloric gain from clams in kcal/gull/h for all age classes at each site in the hypothetical absence of robberies. This conjectural gain was calculated from the average hourly number of captured clams and their caloric contents, the average hourly number of gulls engaged in foraging, feeding and handling of prey, and caloric expenditures for flights to shore to drop and crack clams. The comparison served to determine whether food robbing was profitable.

Means, standard errors and proportions were used to present numerical findings, and differences were tested with the Mann-Whitney *U*-test (Remington and Schork 1970, Conover 1980).

RESULTS AND DISCUSSION

Glaucous-winged Gulls were the only species of gulls present at the study sites. I observed a total of 846 robberies perpetrated on the ground and by aerial chase (Mud Bay N = 428, MacKaye N = 418). None were committed over prey that gulls swallowed with one or two gulps

TABLE 1

EQUATIONS USED TO ESTIMATE CALORIC COST-BENEFITS OF FOOD ROBBING IN GLAUCOUS-WINGED GULLS ON LOPEZ ISLAND, WASHINGTON, 1978

Conjectural caloric gains/gull/h	$= \frac{\text{no. clams captured/h}}{\text{no. foragers/h}} \times (\text{kcal/clam} - \text{kcal/drop flight})$
Caloric gains from captured clams/gull/h	$= \frac{(\text{no. clams captured/h} - \text{no. robbery attempts/h})(\text{kcal/clam} - \text{kcal/drop flight})}{\text{no. foragers/h}}$
Caloric gains from successful ground robberies/robber/h	$= \frac{\text{no. successful ground robberies/h} \times (\text{kcal/clam} - \text{kcal/ground robbery})}{\text{no. robbers/h}}$
Caloric losses from unsuccessful ground robberies/robber/h	$= \frac{\text{no. unsuccessful ground robberies/h} \times \text{kcal/ground robbery}}{\text{no. robbers/h}}$
Caloric gains from successful aerial robberies/robber/h	$= \frac{\text{no. successful aerial robberies/h} \times (\text{kcal/clam} - \text{kcal/aerial chase})}{\text{no. robbers/h}}$
Caloric losses from unsuccessful aerial robberies/robber/h	$= \frac{\text{no. unsuccessful aerial robberies/h} \times \text{kcal/aerial chase}}{\text{no. robbers/h}}$

without processing. The majority (Mud Bay 98%, MacKaye 95%) was committed over clams and the remainder over crabs too large to be swallowed whole. Most ground robberies (Mud Bay 63%, MacKaye 86%) were perpetrated on shores when gulls dropped clams to crack their shells. Most booty (Mud Bay 98%, MacKaye 74%) surrendered by victims in aerial robberies fell to the ground from where robbers retrieved it (the shells invariably cracked upon impact). Therefore, most clams that were obtained by robbing both on the ground or by aerial chase required no further caloric expenditure for drop flights.

Frequencies of robberies were the same at both sites, 0.15/gull/h. However, ground robbery prevailed at MacKaye (69%) whereas robbery by aerial chase was more common at Mud Bay (94%). The usual high density of gulls rendered MacKaye (5.52 gulls/ha/h) conducive to ground robbery. Low density of gulls provided few opportunities for ground robberies at Mud Bay (1.11 gulls/ha/h) because distances between conspecifics handling prey were usually greater than 10 m. The high density of foraging gulls at MacKaye may have been attributable to the close proximity of this site to a nesting colony (2.41 km). Robbers failed in 67% of all attempts to rob at Mud Bay and 51% at MacKaye.

Clams (*Saxidomus* spp., *Tapes* spp., *Clinocardium* spp.) measuring 5–7 cm across their broadest widths were classified as medium while those less than 5 cm in width were small and those greater than 7 cm in width were designated large. At both sites, booty consisted principally of small (Mud Bay 42%, MacKaye 39%) and medium (Mud Bay 46%, MacKaye 42%) clams. The average weight of the meat of clams in a sample of small and medium specimens combined (N = 10) was 10.62 ± 2.26 g. Approximate caloric value of 10.62 g of raw clam meat is 8.16 kcal.

The weighted average durations of drop flights for all age classes were 14.78 ± 0.71 sec requiring 0.15 kcal/drop flight at Mud Bay and 18.91 ± 0.65 sec requiring 0.19 kcal/drop flight at MacKaye. Average durations of aerial chases at Mud Bay were 13.34 ± 0.60 sec for adults, 11.34 ± 0.99 sec for second- and third-year birds, and 15.24 ± 0.78 sec for first-year birds, requiring expenditures of 0.13, 0.11, and 0.15 kcal per chase, respectively. At MacKaye, average durations of chases were 12.31 ± 1.16 sec for adults, 15.22 ± 1.00 sec for second- and third-year birds and 11.00 ± 1.43 sec for first-year birds, requiring expenditures of 0.12 kcal, 0.15 kcal and 0.11 kcal per chase, respectively.

Conjectural caloric gains were 4.90 kcal/gull/h at Mud Bay and 1.64 kcal/gull/h at MacKaye (Table 2). Gulls obtained 3.89 kcal/gull/h from captured clams consumed without threats of robberies at Mud Bay and 0.46 kcal/gull/h at MacKaye. At Mud Bay, robbers gained 0.49 kcal/adult/h, 0.37 kcal/second- and third-year bird/h, and 0.49 kcal/first-year bird/h from

TABLE 2

DATA USED TO ESTIMATE COST-BENEFITS OF FOOD ROBBING IN GLAUCOUS-WINGED GULLS ON LOPEZ ISLAND, WASHINGTON, 1978

Data	Mud Bay Combined age classes	MacKaye Combined age classes
No. clams captured/h	16.2879	17.0294
No. foragers/h	26.6061	82.7647
Kcal/clam	8.1600	8.1600
Average duration of drop flight in sec	14.7663	18.9050
Average caloric expenditure/drop flight	0.1500	0.1900
No. robbers/h	3.3636	12.2941

	adults	age 2 + 3	age 1	adults	age 2 + 3	age 1
No. robbers/h	2.0152	0.3333	1.0152	4.3539	1.4412	6.5000
No. successful ground robberies/h	0.1212	0.0152	0.0606	1.4706	0.5294	3.5882
No. unsuccessful ground robberies/h	0.1061	0.0152	0.0303	0.8824	0.3529	1.7059
Caloric expenditure/ground robbery in kcal	0.0100	0.0100	0.0100	0.0100	0.0100	0.0100
No. successful aerial robberies/h	0.3333	0.0758	0.2273	0.2050	0.0294	0.1765
No. unsuccessful aerial robberies/h	1.4545	0.2273	0.6970	1.7941	0.5294	1.0294
Average duration of chase in sec	13.3418	11.3435	15.2437	12.3081	15.2171	11.0000
Average caloric expenditure/chase	0.1300	0.1100	0.1500	0.1200	0.1500	0.1100

successful ground robberies and lost fewer than 0.01 kcal/robber/h in all age classes for unsuccessful ground robberies. At MacKaye, robbers gained 2.75 kcal/adult/h, 2.99 kcal/second- and third-year bird/h and 4.50 kcal/first-year bird/h from successful ground robberies, and also lost fewer than 0.01 kcal/robber/h in all age classes for unsuccessful ground robberies.

Robbers gained 1.33 kcal/adult/h, 1.83 kcal/second- and third-year bird/h and 1.79 kcal/first-year bird/h from successful aerial robberies at Mud Bay, but lost 0.09 kcal/adult/h, 0.07 kcal/second- and third-year bird/h and 0.10 kcal/first-year bird/h from unsuccessful aerial robberies. At MacKaye, robbers gained 0.38 kcal/adult/h, 0.16 kcal/second- and third-year bird/h, and 0.22 kcal/first-year bird/h from successful aerial robberies, and lost 0.05 kcal/adult/h, 0.05 kcal/second- and third-year bird/h, and 0.02 kcal/first-year bird/h from unsuccessful aerial robberies.

Accordingly, robbers gained a total of 5.61 kcal/adult/h, 6.02 kcal/second- and third-year bird/h, and 6.07 kcal/first-year bird/h at Mud Bay, and 3.54 kcal/adult/h, 3.56 kcal/second- and third-year bird/h, and 5.15 kcal/first-year bird/h at MacKaye. Cost-benefit ratios were smaller for ground robbery than for aerial robbery. Consequently, robbery was more profitable at MacKaye where most robberies were perpetrated on the ground

than at Mud Bay where aerial robbery prevailed. Caloric gains by robbers exceeded conjectural gains by 14% for the adult class, 23% for the second- and third-year class and 24% for the first-year class at Mud Bay, and by 116% for the adult class, 117% for the second- and third-year class, and 214% for the first-year class at MacKaye. The comparison between conjectural caloric gains and gains from captured clams and clams obtained by robbing suggested that robbery, in spite of infrequent successful attempts, was an expedient and advantageous acquisition of food. Gulls exploited conspecifics handling prey and augmented gains from foraging with booty that required no search and no greater, but often fewer, caloric expenditures.

Some first-year birds may have obtained a significant portion of daily food requirements from robbing. Unlike older conspecifics, they occasionally lay in wait for opportunities to rob. At MacKaye, I noticed that first-year birds retreated to shore after having been chased from the mudflat by older conspecifics. Body movements and tilt of their heads indicated that these birds observed drop flights of conspecifics. They dashed toward anticipated drop sites before clams hit the ground. Although first-year birds were outnumbered by older conspecifics at both sites (by a ratio of one first-year bird : two second- and third-year : five adults), they committed a considerable portion of ground robberies at Mud Bay (31%) and most ground robberies at MacKaye (56%). Furthermore, unlike their adult conspecifics, first-year birds exhibited inappropriate behavior upon finding clams. Instead of seizing a clam and flying to shore with it, some of these young birds turned the mollusk over several times, pecked at it, and occasionally abandoned it after having tossed it about. First-year birds dropped clams over the mudflats where the ground was too soft to crack shells and sometimes dropped clams in flight as if having lost a firm grip. Such behavior suggested that shell-cracking is a skill that gulls acquire over time. First-year birds seemingly had few opportunities to improve their skills because older conspecifics repeatedly supplanted them and even chased them from the mudflats. Focal animal sampling revealed that first-year birds were supplanted by adults nine times more frequently than were other adults (N = 43) and that adults captured two clams within shorter time periods (adults: 6.56 ± 1.25 min; second- and third-year birds: 25.72 ± 8.30 min; first-year birds: 21.90 ± 8.46 min) than immature conspecifics ($U = 7.15$, $P = 0.0075$, N = 26).

The methods of my investigation are open to valid criticism and provide merely estimates of cost-benefits in food robbing. Further cost-benefit studies of food robbing should be made with gulls whose identities are known, possibly through color-coded wing tags, to determine whether robbery is a strategy employed by a large proportion of a population at some time or by specific individuals specializing in robbery.

SUMMARY

Cost-benefits of intraspecific food robbing in Glaucous-winged Gulls (*Larus glaucescens*) were investigated to determine whether caloric gains per unit time were greater for robbers than for individuals that did not rob. During 10 weeks, gulls foraging on two clam beds were observed to commit 428 robberies at one study site and 418 at the other. Robberies were committed within and among three age classes of gulls and only over prey that required handling. With exception of some first-year birds, robbers foraged intensively and robbed only when handling of prey rendered nearby conspecifics vulnerable. Minimum caloric gains for robbers were estimated. Caloric expenditures for handling prey and robbing were subtracted from caloric contents of prey. Estimates revealed that caloric gains/h were greater for robbers than for individuals that did not rob. Most robbers augmented gains from foraging. But some first-year birds seemingly acquired crucial portions of daily food requirements from robbing. Suggestions for further study of food robbing were included.

ACKNOWLEDGMENTS

I am grateful to B. J. Verts for assistance with revisions of early drafts, and to J. C. Barlow and R. B. Payne for valuable comments. The study was conducted under the guidance of B. S. Low, my advisor, and G. W. Fowler who assisted with statistical procedures.

LITERATURE CITED

Altmann, J. 1974. Observational study of behavior: sampling methods. Behaviour 49:227–267.

Brockmann, R. J. and C. J. Barnard. 1979. Kleptoparasitism in birds. Anim. Behav. 27:487–514.

Conover, W. J. 1980. Practical nonparametric statistics. 2nd ed. Wiley and Sons Inc., New York, New York.

Hart, J. S. and M. Berger. 1972. Energetics, water economy and temperature regulation during flight. Proc. XV Inter. Ornithol. Congr. The Hague, The Netherlands 15:189–199.

King, J. R. 1974. Seasonal allocations of time and energy resources in birds. Pp. 4–85 *in* Avian energetics (R. A. Paynter, ed.). Nuttall Ornithol. Club 15.

Remington, R. D. and M. A. Schork. 1970. Statistics with applications to the biological and health sciences. Prentice Hall, Englewood Cliffs, New Jersey.

Robbins, C. S., B. Bruun, and H. S. Zim. 1966. Birds of North America. Golden Press, New York, New York.

U.S. Department of Agriculture. 1973. Calories and weight. Washington, D.C.

Vermeer, K. 1963. The breeding ecology of the Glaucous-winged Gulls (*Larus glaucescens*) on Mandast Island, B.C. B.C. Prov. Mus. Occ. Pap. 13.

School of Natural Resources, Univ. Michigan, Ann Arbor 48109. (present address: 4838 Lake Ridge, Apt. TA, Ypsilanti, Michigan 48197.) accepted 30 nov. 1981.

Wilson Bull., 94(3), 1982, pp. 289–296

EFFECT OF FOREST STRUCTURE ON AMERICAN REDSTART FORAGING BEHAVIOR

George E. Seidel and Robert C. Whitmore

American Redstarts (*Setophaga ruticilla*) have been suggested to be an ecologically plastic species (Ficken 1962) which should therefore be able to adapt to a wide variety of habitat types. Removal of timber leads to a variety of forest structures which affect redstart foraging behavior. This study is an attempt to quantify foraging changes in redstarts in response to vegetation structure changes caused by different timber management practices. If changes are noted we also hope to determine specifically which habitat variables affect them.

STUDY AREAS AND METHODS

Fieldwork was conducted in the Fernow Experimental Forest, Tucker Co., West Virginia. The area was cleared of merchantable timber between 1903 and 1911. The United States Forest Service purchased the land in 1915, and in 1916 placed the area under the protection of a Forest Service Unit. In 1934, 1460 ha in the Elk Lick Run drainage was set aside as the Fernow Experimental Forest (Trimble 1977).

Hardwood tree species dominate in this forest. Oaks (*Quercus* sp.) form the most common species group, with northern red oak (*Q. rubra*) the most common species. Other common oaks include chestnut oak (*Q. prinus*), scarlet oak (*Q. coccinea*), and black oak (*Q. velutina*). Sugar maple (*Acer saccharum*), beech (*Fagus grandifolia*), yellow poplar (*Liriodendron tulipifera*), black cherry (*Prunus serotina*), white ash (*Fraxinus americana*), and basswood (*Tilia americana*) are numerous on most sites. Less common species include yellow birch (*Betula lutea*), sweet birch (*B. lenta*), cucumber magnolia (*Magnolia acuminata*), butternut (*Juglans cinerea*), black walnut (*J. nigra*), American elm (*Ulmus americana*), red maple (*A. rubrum*), black locust (*Robinia pseudoacacia*), black gum (*Nyssa sylvatica*), sassafras (*Sassafras albidum*), and sourwood (*Oxydendrum arboreum*).

Two areas, watershed 1 (WS1) (30.0 ha) and watershed 4 (WS4) (38.9 ha) were used in this study. In 1958 almost all trees over 15 cm dbh were removed from WS1, and in 1971 the area was fertilized with 257 kg of urea per ha. WS1 is relatively steep, with 75% of the area having a slope of greater than 21.8°. Timber in WS1 was in the pole stage. WS4 is relatively flat, with all slopes less than 21.8°, and has not been disturbed since 1910. The timber in WS4 is approaching a mature forest.

Singing male redstarts were located in early May 1979, and their locations were marked. Foraging was observed between 06:00 and 10:00 each day throughout the nesting period except on rainy days. The observation procedure consisted of finding a redstart in a marked location and recording data on each foraging maneuver observed. Observation was terminated when the bird was lost from sight or when the bird moved outside of an area which could be covered by a circle 11.3 m in diameter (the size of the vegetational plots to be measured later).

The following information was recorded for each foraging maneuver: (1) foraging maneuver (hawk, glean, or hover [Holmes et al. 1978]), (2) substrate where the maneuver occurred (leaf or branch), (3) substrate species group (oaks, maples, beech, birch, cherries, magnolias, and

all others), (4) branch position where the maneuver occurred (proximal to trunk, middle, distal), (5) height of the maneuver. Variables 2, 3, and 4 were recorded only for gleans or hovers.

Vegetation was measured where foraging had been observed using circular plots in a manner similar to James and Shugart (1970). Variables calculated for each plot included: (1) canopy cover in each of five vertical zones (3.1–6.1 m, 6.1–12.2 m, 12.2–18.3 m, 18.3–24.4 m, and >24.4 m); (2) maximum canopy cover in each vertical zone (percentage of points where vegetation occurred in the given zone, but none occurred in higher zones); (3) percent openings; (4) number of trees per plot <15.2 cm dbh, 15.2–30.5 cm dbh, and >30.5 cm dbh for the species groups mentioned above; and (5) maximum canopy height.

Data were analyzed using univariate and multivariate tests. Student's *t*-test was applied to vegetation variables, using each vegetation plot as a data point. Chi-square and Student's *t*-tests were applied to foraging variables, treating each foraging observation as a data point. Stepwise discriminant analysis was applied to vegetation variables, treating each bird territory as a data point, and to foraging variables after maneuvers; substrates, substrate species group, and branch positions were converted to percent for each bird. A multivariate analysis of variance (MANOVA) was used to obtain the coefficients of the canonical axis at the step of the discriminant analysis in which the best classification occurred.

RESULTS AND DISCUSSION

Data were obtained for 10 males and four females in WS1, and for nine males and three females in WS4. More females were spotted in both watersheds. However, the less conspicuous coloration and lesser amount of physical activity of females made them more difficult to observe than males. Because data were obtained on so few females, analyses were limited to males only.

The results from the univariate tests on vegetation structure variables showed that the mean canopy cover differed between watersheds in all vertical zones except the lowest (Table 1). WS1 had significantly more canopy cover in the second and third vertical zones, while WS4 had significantly more canopy cover in the fourth and fifth zones. WS1 had significantly greater values of maximum canopy cover in the third and fourth vertical zones, while WS4 had significantly more maximum canopy cover in the fifth vertical zone (Table 1). Thus, WS4 had a higher, more open canopy structure than did WS1.

Six vegetation variables entered the stepwise discriminant model at significant ($P < 0.05$) F-values. The variables were, in order of entry: canopy cover in the fifth vertical zone, number of large maples, number of medium beeches, maximum canopy cover in the second vertical zone, canopy cover in the second vertical zone, and number of small oaks. At this point, all territories were classified into the proper watershed, and the difference between watersheds on the basis of vegetation was significant ($F_{6,12} = 100.28$, $P < 0.0001$).

From the coefficients provided by the MANOVA, the canonical axis was calculated. Data points from WS4 grouped higher on the canonical axis

Table 1

Mean and SD of Each Vegetation Variable in Each Watershed[a]

Variable	WS1		WS4	
	Mean	SD	Mean	SD
% canopy cover				
3.1–6.1 m	52.67	19.41	52.71	19.11
6.1–12.2 m	66.96	21.96	54.38	17.71*
12.2–18.3 m	76.96	17.81	54.79	23.52***
18.3–24.4 m	68.04	24.81	84.17	12.04**
>24.4 m	11.79	20.74	76.88	16.14***
Canopy height (m)	24.00	2.80	32.00	3.68***
% openings	17.93	7.85	22.79	7.02*
Percent maximum canopy cover				
3.1–6.1 m	1.25	2.93	0.83	1.90
6.1–12.2 m	4.82	7.51	2.29	3.61
12.2–18.3 m	22.86	24.17	1.67	3.51***
18.3–24.4 m	56.96	29.73	17.92	14.44***
>24.4 m	11.79	20.74	76.88	16.14***
No. trees/plot <15.2 cm dbh				
Oaks	0.36	1.06	0.96	2.51
Maples	7.86	5.12	7.25	6.05
Beech	0.79	1.42	2.38	3.09*
Birches	0.36	0.87	1.04	1.97
Cherries	2.79	3.38	0.00	0.00***
Magnolias	3.07	4.74	0.21	0.59**
Others	2.43	2.90	1.08	2.00
No. trees/plot 15.2–30.5 cm dbh				
Oaks	0.14	0.45	0.38	0.71
Maples	0.75	1.00	0.04	0.20***
Beech	0.00	0.00	0.13	0.34
Birches	0.00	0.00	0.33	0.64*
Cherries	0.29	0.71	0.04	0.20
Magnolias	0.50	0.88	0.13	0.34*
Others	0.71	1.15	0.50	0.72
No. trees/plot >30.5 cm dbh				
Oaks	0.07	0.26	0.58	1.02*
Maples	0.50	0.69	0.33	0.64
Beech	0.00	0.00	0.17	0.48
Birches	0.00	0.00	0.38	0.65**
Cherries	0.07	0.26	0.13	0.45
Magnolias	0.11	0.31	0.17	0.38
Others	0.11	0.31	0.29	0.55

[a] Statistical significance as determined by Student's *t*-test: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. WS1: N = 28; WS4: N = 24.

Table 2

Correlations Between Canonical Axis for Vegetation and Each of the Six Original Variables, and Probability of a Greater Correlation

Variable	r	P (N = 19)
Canopy cover (fifth zone)	0.953	0.0001
Number of large maples	−0.345	0.1486
Number of medium beeches	0.369	0.1195
Maximum canopy cover (second zone)	−0.270	0.2640
Canopy cover (second zone)	−0.377	0.1114
Number of small oaks	0.141	0.5634

than did observations from WS1. A correlation was done between the canonical axis and the six original variables (Table 2). The results from the correlation indicate that the major differences between the two watersheds were that WS4 had more small oaks, more medium birches, and more canopy cover in the fifth vertical zone, while WS1 had more large maples, and more canopy cover and maximum canopy cover in the second vertical zone. These conclusions are possibly erroneous due to the nonsignificance of most of the correlations. However, the fact that all six variables, except number of small oaks, were univariately significantly different between watersheds lends support to these interpretations.

In view of the differences in vegetation between the two areas, the following hypotheses were formulated and tested.

Hypothesis 1.—The more open canopy in WS4 should allow the birds to maneuver more freely in the air, and could possibly allow birds to detect flying prey more easily. Therefore, birds in WS4 should use more hawks and hovers than birds in WS1. The hypothesis tested was that no difference existed in use of foraging maneuvers between watersheds. The hypothesis could not be rejected ($\chi^2 = 0.526$, df = 2, $P > 0.5$, N = 231), indicating that birds in both watersheds used each foraging maneuver with similar frequency.

Hypothesis 2.—WS1 has a lower, more dense canopy cover. The trees in WS1, having shorter branches, would have more leaf area per unit branch length. Therefore, birds in WS1 should forage more from leaves and less from branches than birds in WS4. The hypothesis tested was that no difference existed in leaf or branch use between watersheds. The hypothesis could not be rejected ($\chi^2 = 0.020$, df = 1, $P > 0.5$, N = 162).

Hypothesis 3.—As mentioned before, thickness of vegetation may affect maneuverability of birds. The canopy in WS1 is more compact than that in WS4. Tree crowns in WS1 should be thicker, since natural pruning is

not so advanced in a young forest (Smith 1962). Birds therefore might not move as freely within the tree crowns in WS1, and could therefore forage more efficiently between tree crowns or at the distal branch position. The hypothesis that no difference in use of branch positions existed between watersheds could not be rejected ($\chi^2 = 2.687$, df = 2, $P > 0.1$, N = 162).

Hypothesis 4.—Results from many studies (e.g., MacArthur and MacArthur 1961, Brewer 1963, James 1971, Whitmore 1977, James 1979) indicate that vegetation structure is probably more important to birds than is the vegetation species composition. Since a difference in tree species composition existed between watersheds, a difference in substrate species-use should also exist. The hypothesis that no difference in substrate species-use existed between watersheds was rejected ($\chi^2 = 32.985$, df = 6, $P < 0.005$, N = 162). Greater use of oaks and beeches by birds in WS4 comprised the major part of the difference between areas. Whether or not birds used certain tree species groups in excess of the proportion in which the given group occurred could not be tested, because the volume each tree species occupied in the canopy was not known.

Hypothesis 5.—WS4 had less foliage density in the second and third vertical zones than did WS1. Therefore, birds might forage more frequently in the second and third zones in WS4 than in WS1 because the vegetation structure in these zones imposes less physical interference in WS4. The mean foraging height should, therefore, be greater in WS4 than in WS1. The hypothesis that no difference in foraging height existed between watersheds was rejected ($t = 4.578$, df = 229, 1-tailed $P < 0.0005$).

The first six foraging variables to enter the stepwise discriminant model were amount of foraging in oak trees, amount of use of the distal part of branches, amount of foraging in beech trees, amount of foraging in birch trees, amount of use of the proximal of branches, and average foraging height. Foraging differed significantly between watersheds ($F_{6,12} = 6.24$, $P = 0.0036$). Birds from WS4 grouped higher on the canonical axis calculated from the coefficients provided by the MANOVA than did birds from WS1. Correlations between the canonical axis and each original variable were calculated (Table 3). The only significant correlation was with amount of oak use. Birds in WS4 foraged more in oaks than did birds in WS1.

One might have predicted that the birds would use different tree species in the two study areas. Oaks, beeches, and birches each occurred in amounts significantly different between watersheds in at least one size class. The amount of small oaks and of medium birches each were among the first six variables to enter the discriminant model on the vegetation variables. However, if vegetation structure is more important than tree species composition, as mentioned under Hypothesis 4, it is possible that

TABLE 3

CORRELATIONS BETWEEN CANONICAL AXIS FOR FORAGING AND THE ORIGINAL VARIABLES, AND PROBABILITY OF GREATER CORRELATION

Variable	*r*	*P* (N = 19)
Amount of oak use	0.563	0.0121
Amount of distal branch use	−0.321	0.1796
Amount of beech use	0.429	0.0668
Amount of birch use	0.399	0.0904
Amount of proximal branch use	0.331	0.1659
Mean foraging height	0.449	0.0538

the tree species variables have little biological significance to redstarts. The foraging substrate species may have been determined solely by chance and not by any characteristic of the tree species itself. In view of the above concept, the multivariate analyses on foraging variables were redone, omitting the tree species variables. In this analysis, the variables which best discriminated between the two groups were average foraging height, amount of hawking, and use of the distal branch position. Foraging differed significantly between watersheds on the basis of these variables ($F_{3,15} = 3.96$, $P = 0.0290$). Birds from WS4 grouped higher on the canonical axis calculated from coefficients provided by the MANOVA. The only significant correlation between the canonical axis and the original variables (Table 4) was with average foraging height.

Several questions were generated in view of the above results. Why did birds use essentially the same maneuvers in both areas? Why did no difference exist in leaf or branch use? Why was use of branch positions univariately nonsignificantly different between watersheds, and multivariately nonsignificantly correlated with the canonical axis?

In an attempt to answer these questions another hypothesis was gen-

TABLE 4

CORRELATIONS BETWEEN CANONICAL AXIS FOR FORAGING (WITH TREE SPECIES VARIABLES OMITTED) AND ORIGINAL VARIABLES, AND PROBABILITY OF A GREATER CORRELATION

Variable	*r*	*P* (N = 19)
Amount of hawking	−0.444	0.0568
Amount of distal branch use	−0.421	0.0728
Mean foraging height	0.588	0.0081

erated. Although the vegetation structure differed between areas, perhaps birds foraged in similar habitat in both areas. To test this hypothesis, two new variables were established—canopy cover and percent openings in the vertical zone in which each foraging action occurred. The hypothesis that the mean of each variable was the same in both watersheds was tested using Student's t-test. Neither mean canopy cover ($t = 1.216$, df = 229, $P > 0.2$) nor mean percent openings ($t = 0.641$, df = 229, $P > 0.4$) proved to be significantly different between watersheds. Thus, based on these two variables, the birds seem to have selected similar foraging habitat in both watersheds. Since vegetation in WS1 was more dense than vegetation WS4, birds in WS1 must have picked the more open places in which to forage. The hypothesis that mean percent openings in places of foraging in WS1 did not differ from the overall watershed mean was rejected ($t = 1.876$, df = 125, 1-tailed $P < 0.05$). Thus, birds in WS1 seem to have picked the more open places for foraging.

The fact that birds foraged in similar habitat in both watersheds could explain why little difference in foraging behavior between watersheds was observed. In similar habitat density of prey items and time required to pursue prey (Pulliam 1974) should be roughly equal. Thus, the effects of distance between predator and prey (Schoener 1969) would be similar in both watersheds. The physical effect of vegetation structure on bird movement would also be similar.

SUMMARY

The purpose of this study was to determine how vegetation structure affected the foraging behavior of American Redstarts (*Setophaga ruticilla*). Two watersheds in the Fernow Experimental Forest near Parsons, West Virginia were used as study areas. The first area (WS1) is characterized by pole-stage timber. The second area (WS4) is approaching a mature forest.

Ten male redstarts in WS1 and nine male redstarts in WS4 were used in this study. Foraging observations were taken each morning, weather permitting. Later, vegetation was measured in the place in which foraging occurred.

Overall vegetation differed between areas. WS4 had a taller, less dense canopy than did WS1. WS4 contained more oak, beech, and birch trees, while WS1 contained more cherry, maple, and magnolia trees.

Foraging differed between watersheds only in the height of foraging and in the tree species used. Tree species use, however, possibly was not biologically important. The more open canopy in WS4 allowed birds to forage higher.

Vegetation structure in the place of foraging did not differ between watersheds. Birds in WS1 selected places to forage which had more open vegetation than the overall watershed mean.

ACKNOWLEDGMENTS

We would like to thank G. Lang, E. Harner, and H. Wiant for critically reviewing earlier drafts of this manuscript. E. Harner provided advice concerning the statistical analyses. This

project was supported, in part, by McIntire-Stennis funds from USDA (SEA) and was approved by the Director, West Virginia Agricultural Forestry Experiment Station as Scientific Article No. 1726.

LITERATURE CITED

BREWER, R. 1963. Ecological and reproductive relationships of Black-capped and Carolina chickadees. Auk 80:9–49.

FICKEN, M. S. 1962. Maintenance activities of the American Redstart. Wilson Bull. 74: 153–165.

HOLMES, R. T., T. W. SHERRY, AND S. E. BENNETT. 1978. Diurnal and individual variability in the foraging behavior of American Redstarts. Oecologia 36:141–149.

JAMES, F. C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bull. 83:215–236.

——— AND H. H. SHUGART, JR. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727–736.

JAMES, R. D. 1979. The comparative foraging behavior of Yellow-throated and Solitary vireos:the effect of habitat and sympatry. Pp. 137–163 *in* The role of insectivorous birds in forest ecosystems (J. G. Dickson, R. N. Commer, R. R. Fleet, J. C. Kroll, and J. J. Jackson, eds.). Academic Press, New York, New York.

MACARTHUR, R. H. AND J. W. MACARTHUR. 1961. On bird species diversity. Ecology 42: 594–598.

PULLIAM, H. R. 1974. On the theory of optimal diets. Am. Nat. 108:59–74.

SCHOENER, T. W. 1969. Models of optimal size for solitary predators. Am. Nat. 103:277–313.

SMITH, D. M. 1962. The practice of silviculture. John Wiley and Sons, Inc., New York, New York.

TRIMBLE, G. R. 1977. A history of the Fernow Experimental Forest and the Parsons Timber and Watershed Laboratory. USDA For. Serv. Gen. Tech. Rept. NE–28. Northeast Forest Experiment Station, Upper Darby, PA.

WHITMORE, R. C. 1977. Habitat partitioning in a community of passerine birds. Wilson Bull. 89:253–265.

DIVISION OF FORESTRY, WEST VIRGINIA UNIV., MORGANTOWN, WEST VIRGINIA 26506. ACCEPTED 1 DEC. 1981.

Wilson Bull., 94(3), 1982, pp. 297–302

FACTORS INFLUENCING WINTER DISTRIBUTION AND ABUNDANCE OF TOWNSEND'S SOLITAIRE

Carl E. Bock

In winter, Townsend's Solitaire (*Myadestes townsendi*) is among the most specialized of all North American birds, since it depends almost entirely on the fleshy cones of junipers (*Juniperus*) for food (Lederer 1977a, b; Salomonson and Balda 1977). *Juniperus* spp. is widespread throughout North America (Elias 1980), but the solitaire is restricted in winter to only a portion of that range (A.O.U. Check-list Com. 1957). Many other birds feed upon juniper cones, both in- and outside the solitaire's range, but none appears to be so specialized. The purpose of this study was to attempt to explain why this most specialized juniper-seed predator does not or cannot occupy all regions where its winter food is available.

Grinnell (1914) noted that birds are common only in certain parts of their ranges, which he called centers of abundance. Species' centers of abundance may coincide with areas of maximum resource abundance and diversity. This would be most readily testable in the case of resource specialists, for which the abundance and variety of available resources could be most easily measured. For example, the Acorn Woodpecker (*Melanerpes formicivorus*) is a highly specialized acorn predator, whose centers of abundance coincide with regions of high oak (*Quercus*) species richness and abundance in western North America (Bock and Bock 1974). Presumably a greater variety of available resources increases the probability that at least one will produce a sufficient food crop each year. Acorn Woodpeckers do not normally occupy areas in the west with only one oak species.

In this study, I tested the hypothesis that winter abundance of Townsend's Solitaire is positively correlated with juniper species density and overall abundance. A related hypothesis is that variability in solitaire numbers from year to year would be negatively correlated with juniper species density, because higher resource diversity should reduce the frequency of population declines or emigrations caused by food shortages.

METHODS

Christmas Bird Count (CBC) data on Townsend's Solitaire for the winters of 1962–63 through 1971–72 were combined into 55 latitude-longitude blocks (Fig. 1A), and means and standard deviations of solitaire numbers counted per party-hour per block were computed for the 10-year period. Total CBC sample size for this study was 8129. Distribution maps for 12 species of North American *Juniperus* (from Elias 1980) were superimposed on a single map to determine regional patterns of juniper species density. Abundance of juniper was more difficult to measure. Junipers frequently are mixed as subdominants in various com-

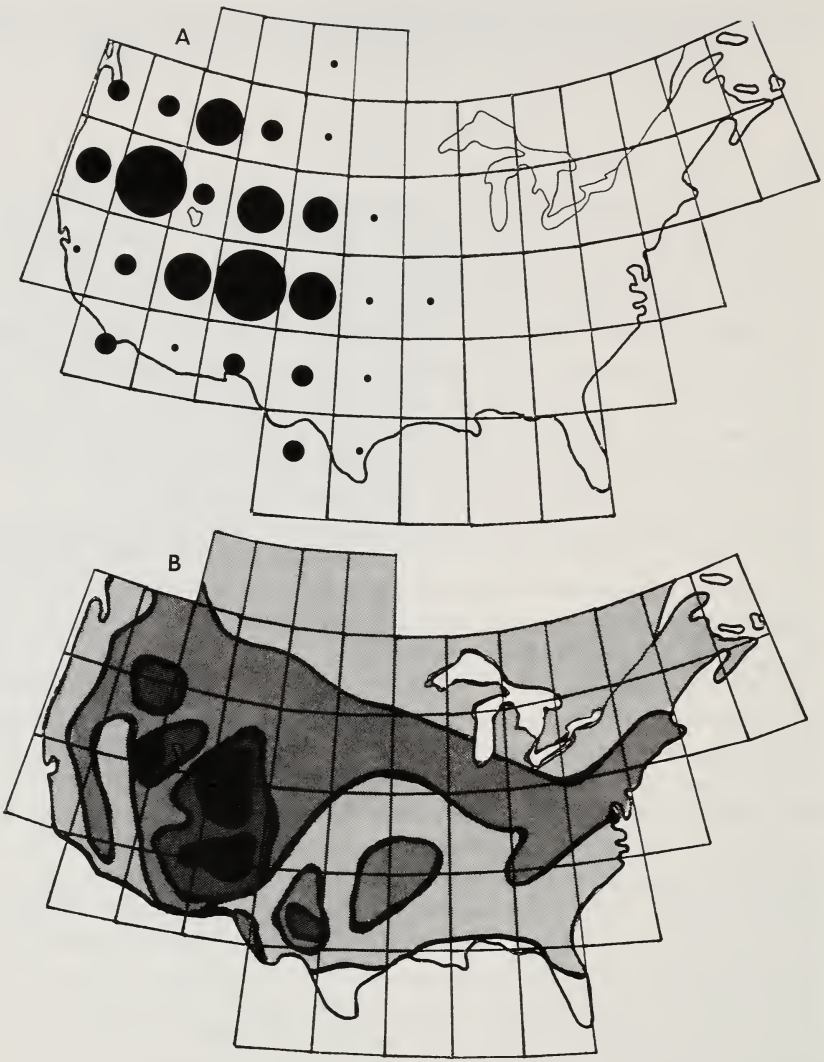


FIG. 1. A. Winter abundance pattern of Townsend's Solitaire, based upon Christmas Bird Count data for 1962–63 through 1971–72. Five sizes of dots represent <0.01 but >0.0, 0.01–0.09, 0.10–0.19, 0.20–0.39, and ≥0.40 birds/party hour. B. Species density of *Juniperus* spp., based upon maps in Elias (1980). Four degrees of shading indicate occurrence of one to four species.

TABLE 1

CORRELATIONS AND PARTIAL CORRELATIONS AMONG SOLITAIRE WINTER ABUNDANCE, JUNIPER SPECIES DENSITY, AND JUNIPER ABUNDANCE

Comparison	Correlation
A. Solitaire abundance vs juniper species density	0.639**
B. Solitaire abundance vs juniper abundance	0.473*
C. Juniper species density vs abundance	0.662**
D. A, with juniper abundance held constant	0.494*
E. B, with juniper species density held constant	0.087

* $P < 0.05$, ** $P < 0.01$.

munity types, but habitat descriptions of CBC circles usually give no indication of their presence or abundance. As an alternative, I calculated the percentage of each 5° block which Küchler (1964) designated as having juniper as dominant or co-dominant potential vegetation.

Pearson product-moment correlation coefficients were calculated comparing the variables (1) mean solitaires per party-hour per block, (2) coefficient of variation of solitaire abundance per block (standard deviation/mean), (3) maximum juniper species density per block, and (4) juniper abundance per block. Sample size was the 26 five degree blocks which recorded solitaires during the 10-year period. Because variables 3 and 4 were highly correlated, partial correlations were computed to look for the independent relationships between solitaire variables and juniper species density vs juniper abundance.

RESULTS AND DISCUSSION

Fig. 1A shows the winter abundance pattern of Townsend's Solitaire, while Fig. 1B shows juniper species density. Correlations between solitaire numbers and junipers are presented in Tables 1 and 2.

Within the range of Townsend's Solitaire, its numbers were significantly higher and significantly less variable as juniper species density increased (Tables 1, 2), supporting both initial hypotheses. Partial correlations among solitaire numbers and variability and juniper abundance

TABLE 2

CORRELATION AND PARTIAL CORRELATIONS AMONG VARIABILITY OF SOLITAIRE ABUNDANCE, JUNIPER SPECIES DENSITY, AND JUNIPER ABUNDANCE

Comparison	Correlation
A. Solitaire variability vs juniper species density	−0.603**
B. Solitaire variability vs juniper abundance	−0.402*
C. Juniper species density vs juniper abundance	0.662**
D. A, with juniper abundance held constant	−0.491*
E. B, with juniper species density held constant	−0.005

* $P < 0.05$, ** $P < 0.01$.

were near 0 (Tables 1, 2). These results suggest that resource diversity is an important factor influencing both the distribution and abundance of Townsend's Solitaire, perhaps more important than resource abundance. Doubtless juniper abundance is important to solitaires on a local scale, but I was unable to measure this relationship with CBC data.

As with the equally specialized Acorn Woodpecker (Bock and Bock 1974), winter abundance of Townsend's Solitaire probably is influenced by both the abundance and the variety of its resources. This principle should apply to all species, namely, that centers of abundance (Grinnell 1914) are coincident with areas where resources are predictable as well as common. More generalized species should be subject to these same biogeographical constraints, but the relationship will be less clear because the variety of suitable resources is greater and difficult to measure. Such generalized species can be expected to have larger and more diffuse centers of abundance.

The winter abundance pattern of Townsend's Solitaire does not fit perfectly with that of juniper species density. In general, the birds appear to be more common in the northwestern portion of the area of high juniper species density than in the south (Fig. 1A, B). Several factors may be responsible for this result. The first is the relationship of the breeding and winter ranges. Solitaires nest north through western Canada to Alaska (A.O.U. Check-list Com. 1957). These northern breeders probably come south in fall only as far as is necessary to find juniper cones in good numbers, thereby accumulating most winters in the northern part of their range. Also, junipers may produce cones more regularly in northern latitudes (R. P. Balda, pers. comm.). Other bird species may influence the winter abundance patterns of the solitaires by competing with them for juniper cones. Competitors include American Robins (*Turdus migratorius*) and bluebirds (*Sialia* spp.) (Lederer 1977a, b; Salomonson and Balda 1977). CBC data show that these species have southerly winter abundance patterns. Mountain Bluebirds (*Sialia currucoides*) are particularly abundant in west Texas (Andrews and Bock 1979), an area of high juniper species density and comparatively low solitaire numbers (Fig. 1A, B).

A final factor which may influence solitaire distribution is juniper palatability. Benedict (1981) has found that solitaires in the Front Range of Colorado greatly prefer cones of *Juniperus scopulorum* over those of the sympatric *J. communis*. Solitaires rarely winter in parts of Canada where only *J. communis* is found, suggesting that cones of this species alone may not represent a suitable food supply. There is evidence that other junipers in the Southwest and Pacific Coast may not produce cones palatable to Townsend's Solitaire (R. P. Balda, pers. comm.).

One null hypothesis for the present study is that the relationship be-

tween solitaire abundance and juniper species density is a coincidence—that the solitaire's winter range is an ecological and evolutionary consequence of some other variable such as climate, competition, or proximity to the breeding range. Correlative studies such as this one cannot rule out this possibility. However, such speculations only beg the fundamental question. Why, among the variety of North American birds which feed on juniper cones, is Townsend's Solitaire alone so specialized? Why are juniper cones in the eastern U.S. eaten only by more generalized frugivores such as robins, bluebirds, waxwings (*Bombycilla* spp.), and Evening Grosbeaks (*Hesperiphona vespertina*)? The only explanation for this, other than historical accident, would seem to be that junipers elsewhere in North America are an unreliable food source upon which to specialize, presumably because the one or two species present fail to produce cones over large areas in large numbers every year.

SUMMARY

Townsend's Solitaire (*Myadestes townsendi*) is a specialized juniper-seed predator. Winter abundance of this species is positively correlated with species density of *Juniperus* spp., while variability in numbers is negatively correlated with the same factor. These results support the hypothesis that species' ranges and centers of abundance are coincident with areas of diverse as well as abundant resources, because such diversity assures that the food supply will be predictable as well as abundant.

ACKNOWLEDGMENTS

I thank Russell P. Balda and Audrey Benedict for their helpful comments. This study was supported in part by NSF grants GB 36860 and DEB 79-10784.

LITERATURE CITED

American Ornithologists' Union Check-list Committee. 1957. Check-list of North American birds, 5th ed. Lord Baltimore Press, Baltimore, Maryland.

Andrews, R. W., and C. E. Bock. 1979. A Christmas bird count analysis of bluebird abundance patterns and population trends. Sialia 1:10–14.

Benedict, A. 1981. Winter territoriality and diet of Colorado solitaires. J. Colorado-Wyoming Acad. Sci. 13:61–62.

Bock, C. E. and J. H. Bock. 1974. Geographical ecology of the Acorn Woodpecker: diversity versus abundance of resources. Am. Nat. 108:694–698.

Elias, T. S. 1980. The complete trees of North America. Van Nostrand Reinhold Co., New York, New York.

Grinnell, J. 1914. Barriers to distributions as regards birds and mammals. Am. Nat. 48: 248–254.

Küchler, A. W. 1964. Potential natural vegetation of the conterminous United States. National Geographic Society, Spec. Publ. No. 36.

Lederer, R. J. 1977a. Winter feeding territories in the Townsend's Solitaire..Bird-Banding 48:11–18.

———. 1977b. Winter territories and foraging behavior of the Townsend's Solitaire. Am. Midl. Nat. 97:101–109.

SALOMONSON, M. G. AND R. P. BALDA. 1977. Winter territoriality of Townsend's Solitaires (*Myadestes townsendi*) in a piñon-juniper-ponderosa pine ecotone. Condor 79:148–161.

DEPT. ENVIRONMENTAL, POPULATION, AND ORGANISMIC BIOLOGY, UNIV. COLORADO, BOULDER, COLORADO 80309. ACCEPTED 1 DEC. 1981.

Wilson Bull., 94(3), 1982, pp. 303–312

MIGRATION PATTERNS OF RED AND NORTHERN PHALAROPES IN SOUTHWEST DAVIS STRAIT AND IN THE NORTHERN LABRADOR SEA

Craig D. Orr, Richard M. P. Ward, Norman A. Williams, and R. G. B. Brown

Red Phalaropes (*Phalaropus fulicarius*) and Northern Phalaropes (*Lobipes lobatus*) are circumpolar shorebirds which breed, with some overlap, in the High and Low Arctic, respectively. In eastern North America the Red Phalarope breeds south to ca. 60°N in Canada and ca. 69°N in Greenland; the corresponding limits are ca. 54°N and ca. 60°N for the Northern Phalarope (Salomonsen 1950/51, Godfrey 1966). Both species winter at sea. Western Hemisphere populations probably migrate to the waters off the west coast of South America (Murphy 1936), though it is possible that Red Phalaropes from eastern North America may also winter off West Africa (Stanford 1953, Brown 1979).

The little that is known of the timing and routes of phalarope migrations comes mainly from sporadic, shore-based observations. Large flocks of Red Phalaropes are regularly reported off New England and Nova Scotia in May or earlier: at the eastern edge of Georges Bank (ca. 41°N, 66°W) from March to May (Lamb 1964; K. D. Powers, pers. comm.); south of Nova Scotia (ca. 43°N, 66°W) on 27 May 1980 (J. F. Kearney, pers. comm.); off Sable Island (ca. 44°N, 60°W) on 29–30 May 1977 (Anon. 1977) and from 31 May–6 June 1980 (E. L. Mills, pers. comm.); in the southern Bay of Fundy (ca. 44°N, 67°W) on 2 June 1981 (R. D. Burns, pers. comm.). Similarly, large numbers of Northern Phalaropes were seen in the Bay of Fundy off Brier Island (ca. 44°15′N, 66°25′W) on 21–23 May 1976 (Anon. 1976). However, few birds of either species remain in southern Canadian waters by the middle of June (Moore 1951, Brown et al. 1975). The first Red Phalaropes reach their breeding grounds between about 28 May–15 June, while northerns arrive a little earlier (Soper 1946, Salomonsen 1950/51, Sutton and Parmelee 1956, Watson 1957, Macpherson and McLaren 1959, Parmelee et al. 1967, Höhn 1971, Mayfield 1979).

There is only a short interval between the end of the phalaropes' spring migration and their return in the fall. This reflects the temporary nature of the pair-bond and the brevity of parental care in these species. Most females leave in early July after they have laid their eggs; the males incubate, and leave in early August, after the young have hatched but before some of them can fly; the juveniles migrate last (Sutton 1932, Salomonsen 1950/51, Tuck and Lemieux 1959, Parmelee et al. 1967, Höhn 1971,

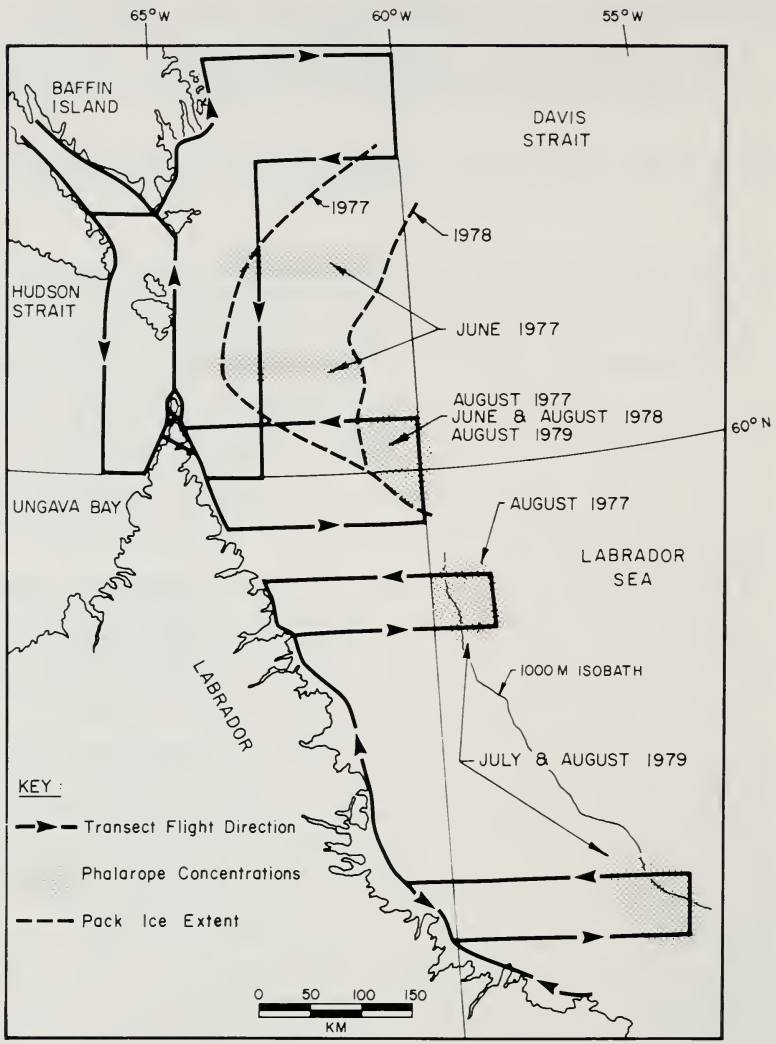


FIG. 1. Aerial survey routes flown off southeast Baffin Island and northeast Labrador in 1978 (north of 59°N) and in 1979 (south of 59°N). The shaded areas give the approximate positions of large concentrations of phalaropes, seen from both aerial and shipboard surveys (see also Table 1, and Brown [1980: Fig. 4]). The 1000-m isobath marks the approximate centre of the Continental Slope.

Kistchinski 1975, Mayfield 1979). Large numbers of Red Phalaropes have been seen off the northern tip of Labrador as early as 22 July (Gross 1937), and birds also return to Newfoundland waters in July (Wynne-Edwards 1935, Brown et al. 1975). They reach a fall staging area off Brier Island in

TABLE 1

MEAN NUMBER OF RED PHALAROPES SEEN DURING 10-MIN SHIPBOARD TRANSECTS AT VARYING DISTANCES OFF NORTHEAST LABRADOR AND SOUTHEAST BAFFIN ISLAND[a]

Date: °N:	5–10 Aug. 1978 54°00′–55°59′	1–9 Aug. 1977 57°45′–58°59′	12–18 Aug. 1977 59°45′–60°30′	18–19 Aug. 1979 60°00′–61°05′	9–20 June 1977 60°56′–64°06′
Distance offshore (km):					
<50	—	*0.4 (5)*	*0.2 (8)*	*0 (7)*	—
50–74	*0 (4)*	*0 (4)*	*0 (4)*	*0 (13)*	*20.2 (6)*
75–99	*0 (2)*	*0 (5)*	*0 (4)*	—	*17.9 (11)*
100–124	*0 (5)*	750.7 (3)	*0 (4)*	—	*13.1 (9)*
125–149	0 (1)	25.0 (2)	30.0 (5)	—	*88.7 (7)*
150–174	75.2 (8)	0 (1)	987.7 (6)	—	4.1 (8)
175–199	0.2 (4)	—	0 (2)	70.8 (6)	4.1 (16)
>200	12.5 (12)	—	0 (1)	5.5 (23)	0.1 (62)
P	<0.05	NS	<0.05	NS	<0.001

[a] Sample sizes are in parentheses. One-tailed probabilities (*P*) refer to Mann-Whitney *U*-tests for the differences between transects inside (italics) and outside the 400-m isobath (August), or inside (italics) and outside the pack-ice zone (June).

late July or early August (R. G. B. Brown, unpubl.). Similarly, Northern Phalaropes arrive off Deer Island (ca. 45°N, 67°W), on the opposite side of the Bay of Fundy, in late July, and numbers there may exceed two million by late August (Vickery 1978). The birds arrive off Cape Cod (ca. 42°N, 70°W) in late July, with a migration peak from the end of August to mid-September (Griscom 1939). Red Phalaropes are scarcer in that area and occur farther offshore, mainly from late August to late September, but with stragglers as late as early November (Griscom 1939, see also Moore 1951).

There is clearly a need for more information on phalarope migration, preferably collected at sea and in a systematic, quantitative way. This paper describes phalarope distributions off northeast Labrador and southeast Baffin Island (55°–64°N; see Fig. 1), based on aerial surveys supplemented by shipboard observations but deals primarily with the Red Phalarope. The two species cannot be distinguished during aerial observations, and it is often hard to identify birds in winter plumage from ships. Nonetheless, it was clear from shipboard observations that the overwhelming majority of birds, including those in all the offshore concentrations (Fig. 1, Table 1), were Red Phalaropes.

METHODS

Aerial survey procedures were similar to those described by Nettleship and Gaston (1978). Fig. 1 shows the transect lines; the area from 59°30′–64°N was surveyed in 1978 and that from 55°–59°N in 1979. In 1978, 18 surveys, each requiring 2 days to complete, were flown

at intervals of 7–10 days from 22 April–5 October, with a final survey on 2 and 6 November. There were 11 surveys in 1979, flown every 2 weeks from 30 May through 12–13 October. The total length of the transect line was 54,750 km in 1978 and 16,582 km in 1979. A DeHavilland Twin-Otter was used in 1978 and a Cessna 337 in 1979 with GNS-500 Global and CMA-734 Omega Navigation systems, respectively (Karant 1976). The aircraft flew 30 m (100 ft) above the sea, at an air speed of 180 km/h (100 kt). The observers sat in the right front (co-pilot's) seat, and in the left rear passenger seat immediately behind the pilot. All birds seen within a 200-m strip on each side of the aircraft were counted and data on species, numbers and activity collected; time and ice cover were noted. All information was taken on cassette tape-recorders. The counts are minimum estimates, since animals are usually under-counted on transect surveys (Eberhardt 1978). To maintain observer efficiency, observation periods never exceeded 2 h (Norton-Griffiths 1976).

Observations were also made from oceanographic survey ships. Birds were counted during 10-min watches while the ship was steaming in excess of 7.6 km/h (4 kt) (Brown et al. 1975). Unlike the aerial surveys, it was not possible to cover transect lines more than once. One cruise was made in the spring (9–20 June 1977) off southeast Baffin Island from ca. 61°W west to the edge of the pack-ice at ca. 63°30′W, along transect lines at ca. 61°N and ca. 63°N (Fig. 1). There were three cruises in late summer off Labrador: 31 July–20 August 1977, 3–12 August 1978, and 10–26 August 1979. All three cruises covered areas from the coast out to the edge of the Continental Shelf. The 1977 and 1978 cruises were north and south of 56°N (Brown 1980: Fig. 5), respectively, and the 1979 cruise from ca. 54°–61°N (R. G. B. Brown, unpubl.).

RESULTS

Spring migration.—Our observations are consistent with the arrival dates reported in the literature (see above). Red Phalaropes were already in southwest Davis Strait when the shipboard survey began on 9 June 1977, and apart from a few stragglers, passage through the area was completed by 16 June. In 1978, the phalaropes arrived between the aerial surveys of 4 and 9 June and numbers peaked in mid-June (Fig. 2). Orr observed phalaropes (predominantly reds) arriving on the tundra around Frobisher Bay settlement, southeast Baffin Island (63°45′N, 68°31′W), in late June 1978.

Concentrations of phalaropes were observed well offshore of southeast Baffin Island and northern Labrador in early June, both during the 1977 shipboard and the 1978 aerial surveys (Fig. 1, Table 1). These birds were just east of the edge of the pack-ice. They appeared to avoid dense pack-ice; almost all (over 90%) were seen in areas where the observers estimated that less than 40% of the surface was ice-covered. The majority of the birds were sitting on the water and probably feeding. Similarly, Macpherson and McLaren (1959) saw large flocks in mid-June at the edge of the landfast ice in northwest Hudson Strait. By mid-June 1978 flocks of phalaropes were flying across stretches of denser pack-ice in Davis and Hudson straits, probably en route to breeding areas farther north and west.

Fall migration.—In 1978 our aerial surveys showed a fairly rapid fall migration off southeast Baffin Island and northeast Labrador (Fig. 2).

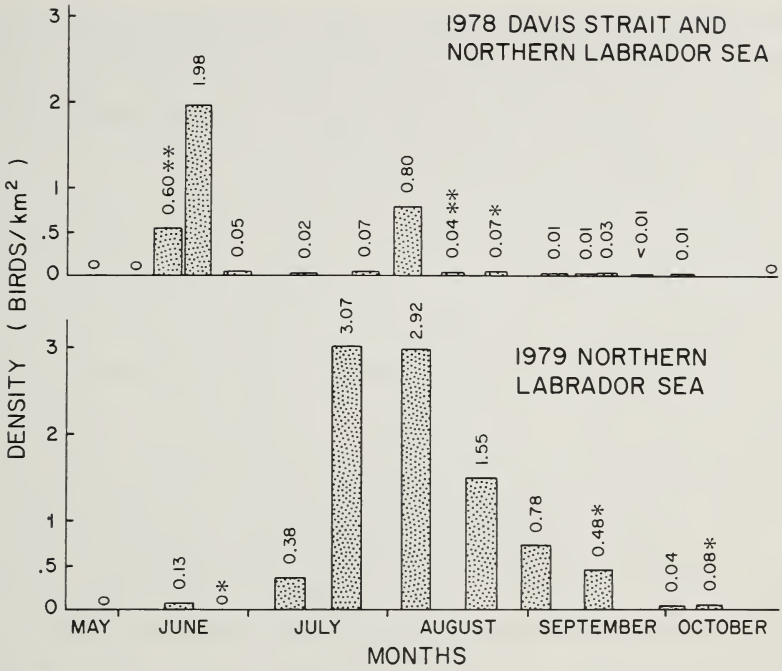


FIG. 2. Seasonal variations in phalarope numbers in the region of the Continental Slope (400–2000-m isobaths) off northeast Labrador and southeast Baffin Island, as shown by aerial surveys in 1978 and 1979. Asterisks indicate surveys in which birds were also seen inshore of the Slope: * <0.05 birds/km²; ** 0.05–0.1 birds/km².

Numbers peaked on the flights on 1–2 August, and very few birds were seen later. In 1979, however, migration off northeast Labrador began earlier, peaking on 24–25 July and 7–13 August. There was a gradual decline after this, but significant numbers of birds remained until early September. The difference between the 2 years may have been at least partly due to viewing conditions; strong winds in July 1978 made the birds harder to see from the air. However, 1978 was an unusually severe summer in the High Arctic, and several species of seabirds either bred late or did not breed at all (D. N. Nettleship, pers. obs.). Another Arctic shorebird, the Semipalmated Sandpiper (*Calidris pusilla*), reached the Bay of Fundy 2–3 weeks later in 1978 than in 1979, and in smaller numbers than usual (P. W. Hicklin, pers. comm.). The numbers of Red Phalaropes off Brier Island were also unusually low in August 1978 (R. G. B. Brown, unpubl.). It is therefore possible that Red Phalaropes did not attempt to breed in the eastern Canadian Arctic in 1978, and instead migrated south, en masse, soon after they arrived.

Even allowing for between-year differences, there appears to be a delay of nearly 2 weeks between the first departures of breeding birds in early July, and the first arrivals in our survey area at the end of that month. The distance to be travelled may account for part of this, but there is also evidence that some birds begin their molt at or near their breeding areas before they set off on migration (Kistchinski 1975).

In both years phalaropes occurred only well offshore during their fall migration down the Labrador coast. On both our aerial and shipboard surveys we found that the birds were virtually confined to the waters above the Continental Slope, between the 400- and 2000-m isobaths (Figs. 1, 2; Table 1). This zone is also at the outer edge of the Labrador Current, and surface water temperatures increase fairly abruptly farther east by ca. 1°–2°C (Brown 1980: Figs. 4, 5). During our 1978 aerial surveys we estimated a peak average density of 5.73 birds/km^2 over the Slope, on 1 August. In 1979 the peak densities over the Slope on our northern and southern transect lines were 1.98 and 23.04 birds/km^2 on 24–25 July, and 6.50 and 17.31 on 7 and 13 August, respectively. The total area of water overlying the Slope from 55°30′N–59°N is ca. 25,000 km^2. If Red Phalaropes were distributed through this zone at an average density of 12.5 birds/km^2 (calculated from the peak densities quoted above), then it is possible that something of the order of 300,000 birds occurred in this zone in late July and early August 1979.

DISCUSSION

Phalaropes at sea feed by sitting on the water and picking at small organisms on or just below the surface (Ridley 1980). Their feeding actions suggest that the birds are aiming at individual prey items. This technique can only be efficient if the density of prey is very high locally. Such conditions occur on the phalaropes' breeding grounds, in the shallow tundra pools where aquatic insects and their larvae are superabundant (e.g., Mayfield 1979), but birds at sea must rely on some oceanographic mechanism to bring their prey to the surface and concentrate it there. The pelagic distributions of both species of phalarope can be interpreted in terms of the occurrence of suitable concentration mechanisms.

Thus, when Red Phalaropes are migrating through southwest Davis Strait (and also in the Bering Sea [Divoky 1979]) in the spring, they are most abundant at or near the edge of the pack-ice. Ice-edge zones are biologically very productive (e.g., McRoy and Goering 1974), and Red Phalaropes are not the only seabirds to exploit them (e.g., Nettleship and Gatson 1978, Bradstreet 1979). The prey found there includes ice-associated crustaceans such as *Apherusa glacialis* and *Onesimus glacialis*, small enough to be taken by birds (e.g., Bradstreet 1980). Red Phalaropes on their way

south through Baffin Bay in the fall are often seen beside icebergs, presumably feeding on this or similar prey (R. G. B. Brown, unpubl.).

However, the birds are more generally associated with 'fronts' and similar boundaries between water bodies when they are at sea farther south, in the fall and winter (Brown 1980). They occur, for example, well offshore of British Columbia, California, Peru, Senegal and Namibia; in all five cases in regions where 'fronts' occur (Murphy 1936, Stanford 1953, Martin and Myres 1969, Ainley 1976, Brown 1979). (Northern Phalaropes occur in the first three of these areas, but closer inshore.) The association between Red Phalaropes and the 'front' at the eastern edge of the Labrador Current has been described above. Zooplankton is trapped and concentrated at the surface in such 'fronts' (Pingree et al. 1974, Brown 1980: Fig. 8), and this is probably what attracts the birds to them, both off Labrador and elsewhere. The ice-edge in southwest Davis Strait and the Labrador 'front' would therefore appear to be potentially rich feeding areas which phalaropes breeding in the eastern North American Arctic may exploit to replenish their energy reserves before embarking on breeding in the spring, molting in late summer or long-distance migration in the fall.

Finally, we conclude from the scarcity or absence of Northern Phalaropes in our survey area that these birds have a different migration route. This species breeds from northern Labrador north to 66°N in Baffin Island (Godfrey 1966), and one would expect their passage between there and the known concentration areas in the Bay of Fundy in spring and fall (see above) to pass through our survey area, if it takes place over the sea. The fact that it apparently does not, seems to indicate an overland migration instead. Northern Phalaropes are known to migrate overland in both western Canada and northwest Europe (e.g., Godfrey 1966, Hildén and Vuolanto 1972), and Richardson (1979) has suggested that part of the eastern Canadian population does so too. The interior of Labrador is virtually uninhabited, and this probably explains why such a passage has gone undetected. It may be that Northern Phalaropes, unlike reds, continue to rely on aquatic insects, their summer food, while they are on their way south in the fall. However, they might also be flying non-stop until they reach the dense concentrations of marine copepods to be found in their staging area in the waters around Deer Island, Bay of Fundy (Fish and Johnson 1937; Vickery 1978; R. G. B. Brown, pers. obs.).

SUMMARY

The timing and routes of the migrations of the Red Phalarope (*Phalaropus fulicarius*) off northeast Labrador and southeast Baffin Island are described from aerial and shipboard surveys made 1977–79. In spring, the birds migrated through the survey area in early and mid-June. The return migration began at the end of July and was completed by mid-August

(1978) or mid-September (1979). Spring migrants were associated with a zone at the edge of the pack-ice, where there was less than 40% ice cover. Fall migrants occurred well offshore, in the area of a 'front' at the outer edge of the Labrador Current, over the Continental Slope. In both cases, the birds were in areas potentially rich in food concentrated at the surface of the water. Northern Phalaropes (*Lobipes lobatus*) were virtually absent, and it is concluded that the population which breeds in northern Labrador and southern Baffin Island migrates overland.

ACKNOWLEDGMENTS

Logistic support and permission to publish these results were provided by Esso Resources Canada Ltd., Aquitaine Co. of Canada Ltd. and Canada Cities Services Ltd. (Davis Strait surveys); Petro-Canada and the oil industry's Labrador Group (Offshore Labrador Biological Studies data); and the Canadian Wildlife Service. Aerial and shipboard observers included J. Brownlie, I. Cameron, D. Gillis, S. Johnson, B. Mactavish, J. Parsons, C. Paton, J. Piatt, M. Purdy, and V. L. Sinclair, as well as the authors. We thank pilots J. MacDonald, R. Michelin, and D. Roy (Bradley Air Services), and F. Fitzpatrick (Labrador Airways), and the ship and scientific personnel of CSS HUDSON and MV LADY JOHNSON II for their help in the field. Computer and statistical assistance was provided by I. Brown; and R. D. Burns, P. Hicklin, J. F. Kearney, S. D. MacDonald, E. L. Mills, D. N. Nettleship, and K. D. Powers gave us unpublished field information. We also thank A. J. Erskine, M. A. Howe, B. Jones, H. F. Mayfield, W. J. Richardson, P. Smith, and D. Stone for their comments on this manuscript. This paper is Report No. 92 of the Canadian Wildlife Service's series 'Studies on northern seabirds'.

LITERATURE CITED

AINLEY, D. G. 1976. The occurrence of seabirds in the coastal region of California. Western Birds 7:33–68.

ANONYMOUS. 1976. The spring migration. Nova Scotia Bird Soc. News. 18:108–138.

ANONYMOUS. 1977. Spring migration. Nova Scotia Bird. Soc. News. 19:153–181.

BRADSTREET, M. S. W. 1979. Thick-billed Murres and Black Guillemots in the Barrow Strait area, N.W.T., during spring: distribution and habitat use. Can. J. Zool. 57:1789–1802.

———. 1980. Thick-billed Murres and Black Guillemots in the Barrow Strait area, N.W.T., during spring: diets and food availability along ice edges. Can. J. Zool. 58:2120–2140.

BROWN, R. G. B. 1979. Seabirds of the Senegal upwelling and adjacent waters. Ibis 121: 283–292.

———. 1980. Seabirds as marine animals. Pp. 1–39 *in* Behavior of marine animals, Vol. IV (J. Burger, B. Olla and H. E. Winn, eds.). Plenum Press, New York, New York.

———, D. N. NETTLESHIP, P. GERMAIN, C. E. TULL, AND T. DAVIS. 1975. Atlas of eastern Canadian seabirds. Can. Wildl. Serv., Ottawa, Ontario.

DIVOKY, G. J. 1979. Sea ice as a factor in seabird distribution and ecology in the Beaufort, Chukchi and Bering Seas. Pp. 9–18 *in* Conservation of marine birds of northern North America (J. C. Bartonek and D. N. Nettleship, eds.). U.S. Fish Wildl. Res. Rept. No. 11.

EBERHARDT, L. L. 1978. Transect methods for population studies. J. Wildl. Manage. 42: 1–31.

FISH, C. J. AND M. W. JOHNSON. 1937. The biology of the zooplankton population of the Bay of Fundy and Gulf of Maine, with special reference to production and distribution. J. Biol. Board Can. 3:189–322.

GODFREY, W. E. 1966. The birds of Canada. Natl. Mus. Can. Bull. 203.
GRISCOM, L. 1939. Migration of the Red Phalarope off Massachusetts. Auk 56:185.
GROSS, A. O. 1937. Birds of the Bowdoin-MacMillan Arctic Expedition. Auk 54:12–42.
HILDÉN, O. AND S. VUOLANTO. 1972. Breeding biology of the Red-necked Phalarope *Phalaropus lobatus* in Finland. Ornis Fenn. 49:57–85.
HÖHN, E. O. 1971. Observations on the breeding behaviour of Grey and Red-necked phalaropes. Ibis 113:335–348.
KARANT, M. 1976. The Global navigation system. Arctic Petroleum Operators Assoc. Pilot 10:59–61.
KISTCHINSKI, A. A. 1975. Breeding biology and behaviour of the Grey Phalarope *Phalaropus fulicarius* in east Siberia. Ibis 117:285–301.
LAMB, K. D. A. 1964. Sea birds of the confluence of the Gulf Stream and Labrador Current east of New York. Sea-Swallow 16:65.
MACPHERSON, A. H. AND I. A. MCLAREN. 1959. Notes on the birds of southern Foxe Peninsula, Baffin Island, Northwest Territories. Can. Field-Nat. 73:63–81.
MCROY, C. P. AND J. J. GOERING. 1974. The influence of ice on the primary productivity of the Bering Sea. Pp. 403–421 *in* Oceanography of the Bering Sea (D. W. Hood and E. J. Kelley, eds.). Univ. Alaska Inst. Mar. Sci. Occ. Publ. No. 2.
MARTIN, P. W. AND M. T. MYRES. 1969. Observations on the distribution and migration of some seabirds off the outer coasts of British Columbia and Washington State, 1946–1949. Syesis 2:241–256.
MAYFIELD, H. F. 1979. Red Phalaropes breeding on Bathurst Island. Living Bird 17:7–39.
MOORE, H. B. 1951. The seasonal distribution of oceanic birds in the western North Atlantic. Bull. Mar. Sci. Gulf Caribbean 1:1–14.
MURPHY, R. C. 1936. Oceanic birds of South America. Am. Mus. Nat. Hist., New York, New York.
NETTLESHIP, D. N. AND A. J. GASTON. 1978. Patterns of pelagic distribution of seabirds in western Lancaster Sound and Barrow Strait, Northwest Territories, in August and September 1976. Can. Wildl. Serv. Occ. Pap. 39.
NORTON-GRIFFITHS, M. 1976. Further aspects of bias in aerial census of large mammals. J. Wildl. Manage. 40:368–371.
PARMELEE, D. F., H. A. STEPHENS, AND R. H. SCHMIDT. 1967. The birds of southeastern Victoria Island and adjacent small islands. Bull. Natl. Mus. Can. 222.
PINGREE, R. D., G. R. FORSTER, AND G. K. MORRISON. 1974. Turbulent convergent tidal fronts. J. Mar. Biol. Assoc. U.K. 54:469–479.
RICHARDSON, W. J. 1979. Southeastward shorebird migration over Nova Scotia and New Brunswick in autumn: a radar study. Can. J. Zool. 57:107–124.
RIDLEY, M. W. 1980. The breeding behaviour and feeding ecology of Grey Phalaropes *Phalaropus fulicarius* in Svalbard. Ibis 122:210–226.
SALOMONSEN, F. 1950/51. Grønlands Fugle. Ejnar Munksgaard, Copenhagen, Denmark.
SOPER, J. D. 1946. Ornithological results of the Baffin Island expeditions of 1928–29 and 1930–31, together with more recent records. Auk 63:1–24, 223–239, 418–437.
STANFORD, W. P. 1953. Winter distribution of the Grey Phalarope *Phalaropus fulicarius*. Ibis 95:483–492.
SUTTON, G. M. 1932. The exploration of Southampton Island, Hudson Bay. Pt. II. Zoology. Sec. 2. The birds of Southampton Island. Publ. Carnegie Mus. 154:1–275.
——— AND D. F. PARMELEE. 1956. On certain charadriiform birds of Baffin Island. Wilson Bull. 68:210–223.
TUCK, L. M. AND L. LEMIEUX. 1959. The avifauna of Bylot Island. Dansk Orn. Foren. Tidsskr. 53:137–154.

Vickery, P. D. 1978. Northeastern maritime region. Am. Birds 32:174–180.
Watson, A. 1957. Birds in Cumberland Peninsula, Baffin Island. Can. Field-Nat. 71:87–109.
Wynne-Edwards, V. C. 1935. On the habits and distribution of birds on the North Atlantic. Proc. Boston Soc. Nat. Hist. 40:233–346.

MacLaren Marex Inc., 1000 Windmill Road, Dartmouth, Nova Scotia B3B 1L7, Canada (CDO, RMPW); MacLaren Marex Inc., P.O. Box 9493, Station B, St. John's, Newfoundland A1A 2Y4 Canada (NAW); Canadian Wildlife Service, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, Nova Scotia B2Y 4A2 Canada (RGBB). (Present addresses: CDO: Dept. Biological Sciences, Simon Fraser Univ. Burnaby, British Columbia V5A 1S6 Canada; RMPW: Dept. Zoology and Inst. Animal Resource Ecology, Univ. British Columbia, Vancouver, British Columbia V6T 1W5 Canada: NAW: Newfoundland and Labrador Dept. Environment, P.O. Box 4750, St. John's, Newfoundland A1C 5T7 Canada). Accepted 15 Nov. 1981.

Wilson Bull., 94(3), 1982, pp. 313–321

RECRUITMENT AND SOCIALLY-SPECIFIC FLOCKING TENDENCIES OF EASTERN SANDHILL CRANES

James R. Lovvorn and Charles M. Kirkpatrick

Nest-sites of Sandhill Cranes (*Grus canadensis*) are widely dispersed and difficult to find. Consequently, annual recruitment (percentage of juveniles) is most easily assessed at concentration areas during winter and migration (Drewien 1973, Lewis 1979). Miller and Hatfield (1974) asserted that counts of flying cranes leaving and returning to roosts gave the least biased estimates of age ratios. Percentages of juveniles in ground counts of cranes on roosts or in feeding fields were lower than in counts of flying cranes near roosts. This difference was attributed to tendency of adults with young to feed away from main flocks and hence be overlooked and undercounted, whereas all social classes of cranes used primary roosts and would be counted during morning and evening feeding flights. Buller (1979) argued that combining all counts of feeding, flying and roosting cranes provided more realistic estimates of annual recruitment. He noted that proportions of young among cranes remaining on refuges during the day were less than among cranes that left refuges to feed.

Young cranes, one or two per family, remain with their parents throughout their first year of life. Although many Greater Sandhill Cranes (*G. c. tabida*) may pair as 2 year olds (Drewien 1973), successful nesting probably does not occur until the third or fourth year (Walkinshaw 1965). Flocks at concentration areas during winter and migration appear to be loosely organized assemblages of smaller groups of one to seven cranes (Miller and Stephen 1966). These groups consist of families or "nonbreeders," which are unsuccessful, or pre-nesting pairs and unmated subadults. The purpose of this study was to investigate differential habitat use and flocking tendencies of family groups vs nonbreeders at an Indiana staging area, and to assess current annual recruitment in the eastern population of Greater Sandhill Cranes. This population breeds in the Lake States and southern Canada, and winters from central Florida north to the Okefenokee Swamp in southern Georgia.

STUDY AREA AND METHODS

The Jasper-Pulaski Fish and Wildlife Area (JPFWA) is 60 km south of Lake Michigan in the sandy lacustrine plain of northwestern Indiana (Jasper and Pulaski counties). Physiography, vegetation, and management history of the area were described by Lovvorn and Kirkpatrick (1981). JPFWA is the primary staging site of the eastern population of Greater Sandhill Cranes, and up to 13,000 cranes may be there simultaneously in fall. Fall roosts are shallow impoundments, often with wooded peripheries, within the refuge area. Cranes

forage in agricultural fields surrounding JPFWA and in the Goose Pasture, a 243-ha refuge feeding field planted in winter wheat, corn and buckwheat. Agricultural fields are continuous and homogeneous in physical aspect, and significant physical boundaries between fields often are lacking. Percentages of cover types available to cranes in fall were roughly 53% corn, 30% soybeans, 3% winter wheat, and 14% fallow and pasture areas. Cranes typically will not feed in corn or soybean fields outside a refuge until after harvesting.

Juvenile (hatching year) Sandhill Cranes are best distinguished from older cranes by characteristic rust-colored plumage on the forehead, occiput and nape; whereas "adult" (after hatching year) cranes have mouse-gray plumage on the occiput and nape, and red, unfeathered skin on the forehead. Lewis (1979) provided details on field discrimination of adults and juveniles. Walkinshaw (1973:84) reported that a captive Greater Sandhill Crane hatched 11 May molted into plumage "quite similar" to that of adults by mid-October. Average hatching dates for 'greaters' passing through JPFWA vary from 10–28 May in southeastern and central Wisconsin to around 24 May in upper-peninsula Michigan and east-central Minnesota (Johnson 1976, Howard 1977, Bennett 1978, Walkinshaw 1978), although northern extent of the range in Canada is unknown. These dates suggest that some juveniles at JPFWA may not be distinguishable from adults after October. However, careful attention to progress of molt indicated that most juveniles could be identified through the second week in November.

Between 13 October and 14 November 1980, a roughly 500-km^2 area centered on JPFWA was surveyed daily from a truck and numbers of juveniles and adults in all aggregations of two or more cranes were recorded. A few counts were made with a 15–60× spotting scope, but most were made at 80× with a window-mounted Questar telescope. Surveys began after 08:30 EST, and lasted until all flocks had been examined or until heat distortions prevented accurate counts. Outside the JPFWA refuge, only counts in which distance, vegetation, lighting and crane activity permitted age classification of all flock members were used for analyses. In the Goose Pasture, however, large numbers of cranes present (up to 4700) and large size of the field (243 ha) at times allowed only samples of age ratios.

During 9–21 October 1979 and 4–17 October 1980, cranes arriving at and departing roosts were characterized as to group size and age composition, and time of arrival or departure. Counts were made with 10 × 50 binoculars from blinds built about 14 m above ground in trees. Families could be distinguished when breaking away from arriving groups just before landing, or before merging with departing groups just after taking flight (Lynch and Singleton 1964, Buller 1979). In most cases, age classification of cranes arriving at roosts was possible until over 90% of the cranes had arrived. Darkness occasionally prevented age discrimination of the last 10–15% of arrivals. Although some cranes probably arrived at or departed roosts during the night, comparisons of evening counts with counts the following mornings indicated such changes were small. Two roosts, Miller Ditch 1 and West Ringneck, were monitored in 1979; and four roosts, Miller Ditch 2 and 3, West Ringneck and West Lake, were monitored in 1980. Water regimes and vegetation at these roosts were described by Lovvorn and Kirkpatrick (1981). Counts of age ratios at roosts were curtailed in late October, when opening of waterfowl hunting season disrupted normal roosting patterns.

RESULTS

Highly significant differences in age ratios of cranes at different roosts were found in both 1979 and 1980 (Table 1). Consistently lower proportions of young were counted in the Miller Ditch roosts, which were separated only by narrow bands of trees, than in West Ringneck and West Lake, which were grouped together 1.6 km away from Miller Ditch. Age ratios

TABLE 1

RESULTS OF RECRUITMENT SURVEYS OF SANDHILL CRANES ARRIVING AT OR DEPARTING ROOSTS, JASPER-PULASKI FISH AND WILDLIFE AREA, 9–21 OCT. 1979 AND 4–17 OCT. 1980

Roost	Year	N	Cranes/count		% juv.[a]	
			$\bar{x}$ SD	Range	$\bar{x}$	SD[b]
Miller Ditch 1	1979	4326	541 ± 275	160–901	11.2	0.2
Miller Ditch 2	1980	3162	395 ± 151	234–621	11.5[c]	0.1
Miller Ditch 3	1980	4322	617 ± 272	149–1029	9.7[c]	0.8
West Ringneck	1979	2702	270 ± 103	135–496	22.4	1.2
	1980	2386	298 ± 215	26–581	19.0[c,d]	2.7
West Lake	1980	4632	926 ± 169	705–1067	15.5[c]	0.4
Total	1979	7028	390 ± 236	135–901	13.4	0.3
Total	1980	14,502	518 ± 301	26–1067	11.9[d]	0.2

[a] (Juveniles/total cranes) × 100.
[b] Weighted by numbers of cranes in each count.
[c] Different from other 1980 roosts, F-test, $P < 0.001$.
[d] Different from 1979, t-test, $P < 0.001$.

at Miller Ditch 1 and 2 and at West Ringneck were similar between years. Overall age ratio was greater in 1979 than in 1980, possibly owing to bias of fewer roosts monitored in 1979.

Water level fluctuations made area of suitable roosting substrate highly dynamic and difficult to measure. Hence, no attempt was made to relate age ratios to numbers of cranes present relative to available substrate. Nevertheless, age ratios were correlated with total cranes counted at roosts during arrival or departure periods ($r^2 = -0.24$, $P < 0.001$). Age ratios also diverged between roosts with progress of arrival period (Fig. 1), suggesting that factors affecting roost preferences of family groups vs nonbreeders became more pronounced as more cranes arrived. Average brood sizes and percent nonbreeders were 1.22 young/pair and 59% in 1979, and 1.16 young/pair and 65% in 1980.

Overall age ratio for ground counts in fields in 1980 was essentially the same as for combined roost counts (Table 2). Lower proportions of young were found among cranes remaining in the Goose Pasture during the day than among cranes leaving the refuge to feed. Considerable variation in daily totals apparently resulted from daily differences in numbers of nonbreeders remaining in the Goose Pasture. When large flocks, with high proportions of nonbreeders, remained in the Goose Pasture, age ratios outside the refuge were inflated. Because cranes in the Goose Pasture were undersampled when flock sizes there were large, age ratios from combined field and refuge counts over-reflected changing ratios outside the refuge.

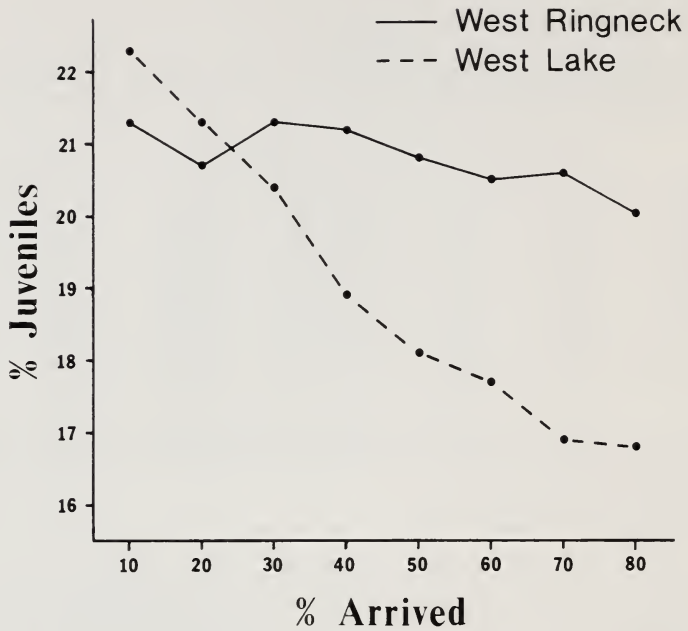


FIG. 1. Mean percentages of juveniles among Sandhill Cranes having arrived at West Ringneck and West Lake roosts at different stages of five arrival periods, Jasper-Pulaski Fish and Wildlife Area, October 1980.

TABLE 2

RESULTS OF RECRUITMENT SURVEYS OF SANDHILL CRANES IN FIELDS, JASPER-PULASKI FISH AND WILDLIFE AREA, FALL 1980

Date	N	% juv.[a] Off refuge $\bar{x}$ SD[b]	Goose Pasture $\bar{x}$ SD[b]	Daily totals $\bar{x}$ SD[b]	Range	Mean flock size off refuge	Staging numbers[c]
Oct. 13–20	13,333	11.8 ± 0.7	7.6[d] ± 0.7	10.9 ± 0.2	9.8–13.8	110	9500
Oct. 26–31	19,627	12.3 ± 0.6	9.8[d] ± 1.8	11.9 ± 0.5	9.8–14.2	162	10,900
Nov. 2–7	9795	13.9 ± 0.6	11.7[d] ± 1.0	13.1 ± 0.1	12.3–14.3	108	9900
Nov. 8–14	15,867	15.9 ± 1.1	10.2[d] ± 0.7	13.0 ± 0.4	10.2–14.2	145	8200
Total	58,622	13.1 ± 0.8	10.0[d] ± 0.9	12.2 ± 0.5	9.8–14.3	133	—

[a] (Juveniles/total cranes) × 100.
[b] Weighted by numbers of cranes counted each day.
[c] Midpoint for period extrapolated from weekly counts.
[d] Different from off refuge, *t*-test, $P < 0.005$.

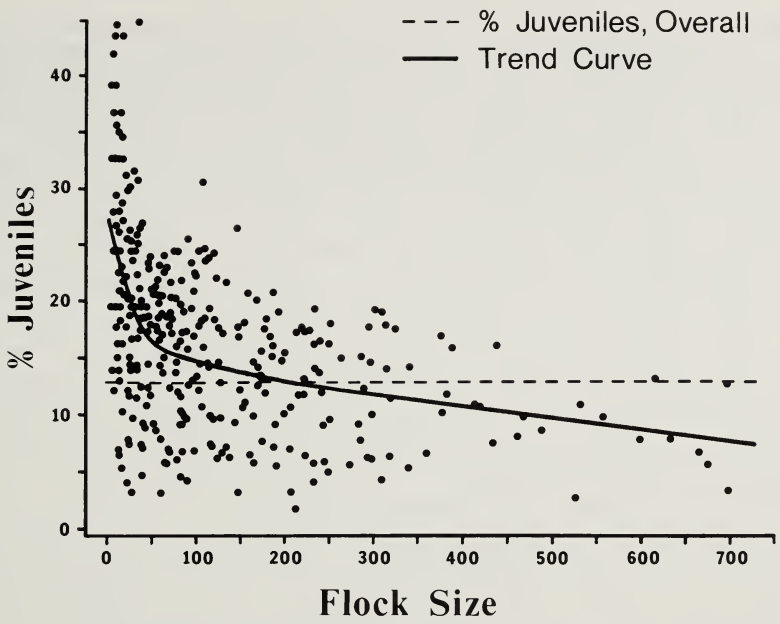


FIG. 2. Relationship between percentage of juveniles and flock sizes of Sandhill Cranes outside the refuge, and percentage of juveniles for the total off-refuge sample, Jasper-Pulaski Fish and Wildlife Area, October–November 1980.

The curve in Fig. 2 was constructed piecewise by linear and nonlinear least squares regressions over intervals of homogeneous variances. The plot indicates that variability and magnitude of age ratios declined as flock sizes increased. Comparing the curve with overall age ratio suggests that sampling primarily flocks of <150 cranes could cause substantial overestimates of annual recruitment.

DISCUSSION

Protection from predators and enhanced foraging efficiency are foremost among sundry hypotheses for adaptive value of bird flocks (Moriarty 1976). Observed flock sizes may result from individuals balancing costs and benefits of flocking behavior. Lovvorn and Kirkpatrick (1982b) found that previous crane use of a field both within and between years was the best predictor of where large crane flocks occurred at JPFWA in fall. This site fidelity was essentially independent of crop type, distance from roosts, or weather, and appeared to result from regimes of human disturbance. The continuous, homogeneous nature of agricultural land in northwestern Indiana argues against enhanced food-finding as a basis for flocking in fall,

although historically food may have been more patchy. Cranes leave their roosts in small groups and join flocks upon reaching feeding fields (Miller and Stephen 1966, this study). Cranes apparently continue to join such flocks until foraging competition or social tensions offset disturbance-avoiding benefits of joining large flocks in consistently undisturbed fields. In such repeatedly used fields, food in fact may have been much reduced.

Among survival benefits of avian family cohesion are enhanced feeding time for juveniles while adults remain alert, and social dominance over non-family individuals (Prevett and MacInnes 1980). Juvenile cranes spend more time actively foraging and less time watching the surrounding area than adults (Miller and Hatfield 1974). Maintenance of higher foraging rates of juveniles may require larger foraging areas, possibly resulting in more frequent aggressive interactions for families in large flocks. Families are consistently dominant over nonbreeders, but avoidance behavior may require less energy than aggressive behavior, causing families to seek better foraging conditions by avoiding large flocks.

Moreover, negative relation of age ratio with flock size also held for cranes on roosts, where foraging efficiency was no longer pertinent. Although early arrivals at roosts were primarily families whose juveniles often foraged actively, most foraging soon ceased as more cranes arrived (Lovvorn and Kirkpatrick 1981). It appeared that many families landed first in West Lake, but later in the arrival period moved to nearby West Ringneck as numbers of cranes in West Lake became large (Fig. 1, Table 1). Much aggression was evident during roost arrival periods, and cranes landing within 2 m of other cranes on the ground were almost invariably pecked at by the previous arrivals. Nevertheless, cranes at given roosts typically aggregated into single roosting clusters, within which quite uniform individual distances were maintained, while leaving substantial areas of suitable roosting substrate unoccupied. These behaviors suggested that advantages of flocking, presumably related to predator detection and avoidance, were strong, and that density of roosting cranes was less of a limiting influence to families than absolute flock size. Prevett and MacInnes (1980) noted that members of Snow Goose (*Anser caerulescens*) families were more easily separated during migration when concentrated in large flocks on refuges. Family members often became separated in the confusion when large numbers of birds flushed simultaneously. Such risks of separation may influence crane families to avoid larger flocks when feeding or roosting, regardless of quality or quantity of substrate.

Sandhill Cranes nesting in southern Michigan, which form <10% of the estimated eastern population and probably do not pass through JPFWA (Lovvorn and Kirkpatrick 1982a), had an average recruitment of 19.4% during 1952–1958 (Walkinshaw et al. 1960) and 14.0% in 1971–1973 (Walkinshaw and Hoffman 1974). Crane age ratios at JPFWA were about 13%

(N [of cranes counted] = 525) in 1976 (Crete 1980), 10.3% (N = 4861) (Crete 1980) to 11.3% (N = 9894) (Bennett 1978) in 1977 and about 12% in 1980 (this study). Current annual recruitment of the eastern population of Greater Sandhill Cranes apparently is 10–13%. Drewien (1973) suggested that recruitment of 13–14% among Greater Sandhill Cranes at Grays Lake, Bonneville Co., Idaho, characterized an increasing, expanding population; whereas the population in southeastern Oregon was considered stable with recruitment of 8–10% (Littlefield and Ryder 1968). Age ratios suggest that the recently growing population in the Lake States and southern Canada (Lovvorn and Kirkpatrick 1982a) may be approaching stability at least in some portions of the range.

Age ratios must be interpreted with care, however. High proportions of young could result from scarcity of subadults in adult plumage, whereas low ratios could result from exceptional production 1–3 years earlier (Prevett and MacInnes 1980). Data on brood sizes obtainable through counts at roosts allow inferences concerning age structure as well as annual recruitment. Trends in proportions of nonbreeders could not be evaluated in this study, as average brood sizes were not determined in previous investigations at JPFWA.

Age ratio data must be collected in light of potential sampling bias. Fluctuations in numbers of nonbreeders remaining in refuge feeding fields where complete counts are not feasible may cause marked variability in observed age ratios. This phenomenon necessitates repeated sampling on different days in the same area. Roost counts should include samples from different roosts, and ground counts in fields should not favor small flocks even though they are more easily and accurately counted.

SUMMARY

Annual recruitment and differential flocking tendencies of family group vs nonbreeding Sandhill Cranes (*Grus canadensis*) were studied at the Jasper-Pulaski Fish and Wildlife Area, Indiana, in the autumns of 1979 and 1980. Highly significant differences in age ratios of cranes at different roosts were found in both years. Age ratios at roosts were negatively correlated with total cranes counted during arrival or departure periods. Age ratios at different roosts diverged with progress of arrival period, suggesting that factors affecting roost preferences of family groups vs nonbreeders became more pronounced as more cranes arrived.

Overall age ratio for ground counts in fields in 1980 was essentially the same as for combined roost counts. Total age ratios in fields showed considerable daily variation. This variation apparently resulted from daily differences in numbers of nonbreeders remaining in refuge fields, where large flocks were undersampled. Outside the refuge, variability and magnitude of flock age ratios declined as flock sizes increased.

Current annual recruitment of the eastern population of Greater Sandhill Cranes is probably 10–13%. Age ratios must be interpreted carefully, relative to inferred population structure and potential bias in sampling procedures.

ACKNOWLEDGMENTS

We thank D. E. Jessup, property manager at JPFWA, Indiana Division of Fish and Wildlife, for allowing access to the study area. This work was supported by the Accelerated Research Program for Migratory Shore and Upland Game Birds, U.S. Fish and Wildlife Service, through contract 14-16-0009-79-005 with the Indiana Department of Natural Resources, Division of Fish and Wildlife. G. W. Archibald, G. S. Libey, H. G. Lumsden and H. P. Weeks, Jr., reviewed the manuscript. This is Journal Paper 8472 from Purdue University Agricultural Experiment Station.

LITERATURE CITED

BENNETT, A. J. 1978. Ecology and status of Greater Sandhill Cranes in southeastern Wisconsin. M.S. thesis, Univ. Wisconsin, Stevens Point, Wisconsin.

BULLER, R. J. 1979. Lesser and Canadian Sandhill crane populations, age structure, and harvest. U.S. Fish and Wildl. Serv. Spec. Sci. Rept.–Wildl. 221.

CRETE, R. A. 1980. Biology of Greater Sandhill Cranes in Burnett County, Wisconsin. M.A. thesis, St. Cloud State College, St. Cloud, Minnesota.

DREWIEN, R. C. 1973. Ecology of Rocky Mountain Greater Sandhill Cranes. Ph.D. diss., Univ. Idaho, Moscow, Idaho.

HOWARD, T. J. 1977. Ecology of the Greater Sandhill Crane in central Wisconsin. M.S. thesis, Univ. Wisconsin, Stevens Point, Wisconsin.

JOHNSON, J. M. 1976. Territory, nesting, and habitat utilization of Greater Sandhill Cranes in Morrison County, Minnesota. M.A. thesis, St. Cloud State College, St. Cloud, Minnesota.

LEWIS, J. C. 1979. Field identification of juvenile Sandhill Cranes. J. Wildl. Manage. 43: 211–214.

LITTLEFIELD, C. D. AND R. A. RYDER. 1968. Breeding biology of the Greater Sandhill Crane on Malheur National Wildlife Refuge, Oregon. Trans. N. Am. Wildl. Nat. Resour. Conf. 33:444–454.

LOVVORN, J. R. AND C. M. KIRKPATRICK. 1981. Roosting behavior and habitat of migrant Greater Sandhill Cranes. J. Wildl. Manage. 45:842–857.

——— AND ———. 1982a. Fall census of eastern Greater Sandhill Cranes. Pp. 259–265 *in* Proc. Int. Crane Workshop.

——— AND ———. 1982b. Field use by staging eastern Greater Sandhill Cranes. J. Wildl. Manage. 46:99–108.

LYNCH, J. J. AND J. R. SINGLETON. 1964. Winter appraisals of annual productivity in geese and other water birds. Wildfowl Trust Ann. Rept. 15:114–126.

MILLER, R. S. AND J. P. HATFIELD. 1974. Age ratios of Sandhill Cranes. J. Wildl. Manage. 38:234–242.

——— AND W. J. D. STEPHEN. 1966. Spatial relationships in flocks of Sandhill Cranes (*Grus canadensis*). Ecology 47:323–327.

MORIARTY, D. J. 1976. The adaptive nature of bird flocks: a review. Biologist 58:67–79.

PREVETT, J. P. AND C. D. MACINNES. 1980. Family and other social groups in Snow Geese. Wildl. Monogr. 71.

WALKINSHAW, L. H. 1965. Territories of cranes. Michigan Acad. Sci., Arts, Letters L: 75–88.

———. 1973. Cranes of the world. Winchester Press, New York, New York.

———. 1978. Sandhill Crane studies in Michigan's upper pensinula. Jack-Pine Warbler 56:107–121.

——— AND R. H. HOFFMAN. 1974. Southern Michigan Sandhill Crane survey, 1971–1973. Jack-Pine Warbler 52:102–114.

———, W. P. COTTRILLE, AND B. D. COTTRILLE. 1960. Southern Michigan Sandhill Crane survey, 1952–1958. Jack-Pine Warbler 38:25–28.

DEPT. FORESTRY AND NATURAL RESOURCES, PURDUE UNIV., WEST LAFAYETTE, INDIANA 47907. (PRESENT ADDRESS JRL: SCHOOL OF NATURAL RESOURCES, UNIV. MICHIGAN, ANN ARBOR, MICHIGAN 48109.) ACCEPTED 15 DEC. 1981.

Wilson Bull., 94(3), 1982, pp. 322–328

EFFECTS OF CONTEXTUAL INFORMATION ON BEHAVIOR OF *CALIDRIS* SANDPIPERS FOLLOWING ALARM CALLS

Daniel W. Leger and Jami L. Nelson

Two classes of individuals—signalers and recipients—exist in all animal communication systems (Wilson 1975, Smith 1977). Signals make information available and recipients use this information when "choosing" a response (e.g., Leger and Owings 1978; Seyfarth et al. 1980a, b). Contextual information, which exists outside signals, is also usually available to recipients and may be appraised by them when selecting a response (Smith 1965, 1977). Consequently, to fully understand the responses of recipients we must identify contextual information in addition to signal-conveyed information.

Vertebrate "alarm" signals (signals emitted in the presence of potential predators) may be multi-functional and appear to vary interspecifically in information content. Some, such as the "hawk alarm" calls of small passerines, may only inform others that a raptor has been detected, but not inform recipients of the hawk's or the caller's locations (Charnov and Krebs 1975). In contrast, the alarm calls of other species, including vervet monkeys (*Cercopithecus aethiops*) and California ground squirrels (*Spermophilus beecheyi*), provide extensive information about the type of predator, the location of the caller and even the callers' age and sex (Seyfarth et al. 1980a, b; Leger et al. 1980; Owings and Leger 1980). Regardless of the type and amount of information contained in alarm signals, it would seem beneficial for recipients to appraise as much contextual information as possible, because of the serious danger posed by predators.

An important form of contextual information for alarm call recipients is the individual's vulnerability at the time the signal is detected. In fact, recipients of alarm calls do behave differently when vulnerable than when relatively safe (e.g., beaver [*Castor canadensis*] [Hodgdon and Larson 1973], vervet monkeys [Seyfarth et al. 1980a, b], California ground squirrels [Leger et al. 1979], hoary marmots [*Marmota caligata*] [Noyes and Holmes 1979]).

Shorebirds feeding on mudflats adjacent to marshy areas are exposed to attacks by raptors which may use marsh vegetation for concealment during their approach (Rudebeck 1950, 1951; Hunt et al. 1975; Page and Whitacre 1975; Dekker 1980). When they detect predators, shorebirds utter loud calls that usually elicit immediate flock formation and synchronous, erratic flight (Owens and Goss-Custard 1976). "False alarms," i.e., calls occurring in the apparent absence of predators, are also fairly com-

mon in shorebirds (Leger, pers. obs.). If most attacks by raptors come from the direction of the marsh vegetation, and if the vision of shorebirds is partly occluded by the vegetation, we would expect that individuals closest to the vegetation would be most vulnerable to attack. Thus, individuals hearing alarms while near the marsh should take immediate anti-predator action. Shorebirds farther from the marsh might be able to look around for the predator, and, not finding one, resume foraging. This study was conducted to determine whether shorebirds vary their responses to alarm calls as a function of their distance from the predator-concealing marsh.

METHOD

Subjects and study site.—Response to alarm call playbacks was studied in two species of wintering shorebirds, the Western Sandpiper (*Calidris mauri*) and the Dunlin (*C. alpina*). As the tide recedes, these and other shorebird species assemble to feed on mudflats adjacent to the marsh (Recher 1966). They risk predation by Northern Harriers (*Circus cyaneus*) and Kestrels (*Falco sparverius*), both of which often hunt shorebirds by flying fast and low over the marsh, then suddenly bursting out over the mud to catch their prey by surprise.

This experiment took place in February 1980 along San Francisco Bay at the Baylands Nature Area, in Palto Alto, San Mateo Co., California. The Baylands has a wooden walkway, slightly elevated over the marsh vegetation. At some points the walkway projects out over the mudflat, permitting views of the marsh/mud interface. The specific study site was a section of mudflat with a nearly straight line of marsh vegetation abutting it. Shorebirds at this site seem unresponsive to stationary humans.

Equipment and procedure.—Two months before the experiment, Leger recorded ca. 1.5 sec of alarm calls given by American Avocets (*Recurvirostra americana*) in response to a harrier flying nearby. The recording was made on a Uher 4400 recorder with Uher microphone at 19 cm/sec tape speed. Field observations indicated that such calls usually evoked generalized escape reactions in all shorebirds.

In the morning, before the receding tide had exposed any mud, playback equipment was set up on a section of boardwalk that was elevated about 2.5 m above the mud surface and about 20 m from the marsh vegetation. The playback speaker was oriented from the mudflat toward the marsh. As the water receded, shorebirds began assembling on elevated areas of marsh. As soon as some mud was exposed birds began foraging there. When a 2–3-m strip of mud adjacent to the vegetation was exposed, we began playbacks of either avocet calls (N = 10) or a comparable segment of blank audiotape (designated as "no-sound") as a control for the movements associated with equipment operation (N = 7). Playbacks used the Uher 4400 recorder and an Electrosonics "Voice-Projector" amplifier with its integral speaker. Playback volume was adjusted in advance so that it approximated (by ear) that of naturally occurring avocet calls. Immediately before each playback, the area was photographed with a tripod-mounted 35-mm camera (Olympus OM1) equipped with a 100-mm lens and slide film. Immediately after taking the photograph and advancing the film, a playback occurred. Within 1 sec following the end of a playback, a second photograph was taken of the same area. Alarm and no-sound playbacks were alternated with at least 5 min between playbacks. Also, at least 5 min elapsed following naturally occurring alarms of any species, and trials were aborted if an alarm call occurred between the first photograph and the playback.

Because many shorebirds followed the receding tide, only a few playbacks could be done

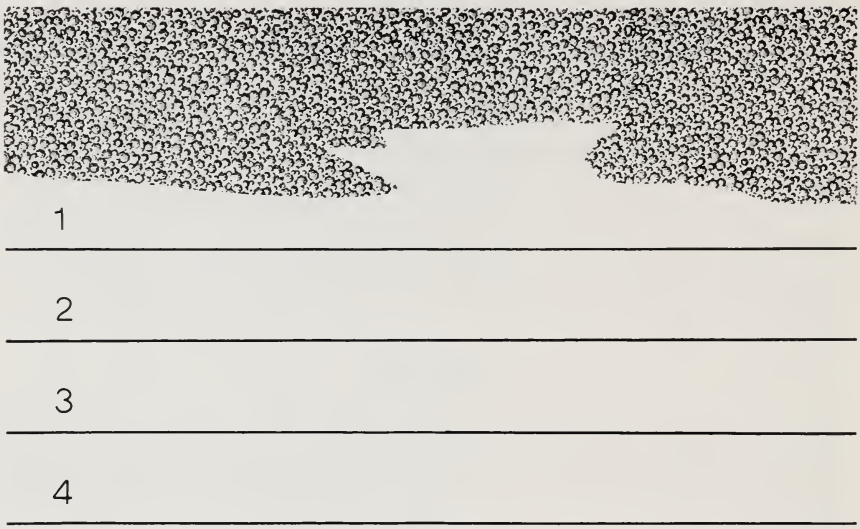


FIG. 1. Outline map of the study site as viewed through the camera. The white area is mudflat and the darker area is marsh vegetation. The parallel lines drawn through the mudflat are ca. 0.5 m apart.

each day before the number of birds in the field of view became too small. Thus, the experiment was conducted on 4 different days during a 3-week period.

Data analysis.—We projected the slides onto outline maps of the marsh and marked the locations of all birds, as well as their postures (head-up or head-down [probing]). We could not obtain exactly the same camera placement each day, so a separate map was drawn for each day's view.

The outline maps (Fig. 1) included straight lines drawn approximately parallel to the edge of the marsh and ca. 0.5 m apart. The distance between adjacent lines was estimated by scaling the standing height of dowitchers (*Limnodromus*) and Dunlins from the slides according to heights measured on mounted museum specimens. From the Dunlin scale the lines were judged to be ca. 53 cm apart; from the dowitcher scale they were ca. 49 cm apart. We used these "strips" to reference birds' locations progressively farther from the marsh. Dependent variables included (1) the number of birds in each strip, (2) the total number of birds, and (3) the percentage of birds in head-up postures. Unless indicated otherwise, statistical tests are 2-tailed *t*-tests for correlated means.

Because it was extremely difficult to consistently distinguish *C. mauri* from *C. alpina* on the slides and because some Least Sandpipers (*C. minutilla*) were probably photographed and counted, our data are for *Calidris* species combined. Larger shorebird species, primarily dowitchers and plovers (*Charadrius vociferus, C. semipalmatus*), were also photographed. Unfortunately, the numbers of these larger species varied substantially from day-to-day and their density in the camera's field of view dropped precipitously during a field session (due to the pronounced tendency of dowitchers to forage in the receding water). Therefore, we have too few data on a species other than *Calidris* for meaningful analysis.

TABLE 1

MEAN NUMBER OF *CALIDRIS* SANDPIPERS ON EACH STRIP OF MUDFLAT BEFORE AND AFTER PLAYBACKS OF AVOCET ALARM CALLS OR NO-SOUND (CONTROL) PLAYBACKS

	Alarm call		No sound	
Strip	Before	After	Before	After
1	5.4	2.9*	5.3	6.1
2	5.3	5.0	6.3	5.1
3	2.0	2.1	2.4	2.4
4	1.7	1.0	0.6	0.9

* $P < 0.02$.

RESULTS

Before alarm playbacks (N = 10), an average of 14.4 *Calidris* was counted in strips 1–4 combined, and before no-sound playbacks (N = 7) a similar mean of 14.6 birds was present in each strip. Birds were not equally distributed among the four strips: strips 1 and 2 averaged 5.4 and 5.7 *Calidris*, respectively, whereas strips 3 and 4 (farther from the marsh) averaged 2.2 and 1.2, respectively. These means differed significantly ($F = 8.64$; df = 3, 45; $P < 0.01$ split-plot factorial analysis of variance [Kirk 1968]). However, there was no significant interaction between distance from marsh and playback condition ($F = 0.33$; df = 3, 45; NS).

Following alarm playbacks there was an average net loss of 3.4 birds from the total area (from 14.4–11.0), but the mean totals before vs after playback did not differ ($t = 1.08$, df = 9, $P < 0.20$). However, strip 1 had only 53.7% as many *Calidris* following alarm calls as before ($t = 2.87$, df = 9, $P < 0.02$). Net losses in the other three strips were not significantly different (Table 1). In contrast there was no significant net loss of birds following no-sound playbacks, and none of the before vs after playback comparisons were statistically significant (Table 1). The latter indicates that experimenter movements while operating the camera and playback equipment did not measurably alter the birds' behavior.

Significantly more birds were head-up after alarm call playbacks (68.0%) than before (32.4%) ($t = 2.64$, df = 7, $P < 0.05$; two trials were dropped from this analysis because all birds left the field of view following playbacks). In contrast, 29.4% of all birds were head-up after no-sound playbacks, but 45.9% were head-up before. This difference was non-significant, however ($t = 1.36$, df = 6, $P < 0.20$). Head-up posturing also varied with distance from the marsh following alarm playbacks. In strips 1 and 2, 69% and 62% of the birds were head-up, respectively, as compared with 38% and 40% in strips 3 and 4.

DISCUSSION

These data suggest that *Calidris* sandpipers monitor their distance from the marsh edge and use this information when responding to alarm calls. It is intriguing that individuals farther from the source of the alarm, but closer to the marsh, reacted more vigorously than did birds in the reverse situation. This finding supports the notion that sandpipers view the marsh as a source of potential danger. Moreover, sandpipers behave as though alarm calls are indicative of danger from the direction of the marsh. At no time did birds fly toward the marsh in response to playbacks or naturally occurring calls. This differs dramatically from the behavior of Yellow-eyed Juncos (*Junco phaeonotus*) foraging at varying distances from a small tree. They use the tree as a refuge, flying to it when alarmed (Caraco et al. 1980). Presumably they would also be more likely to take flight the farther they are from vegetation.

Our data also suggest that there may be some critical distance from the edge of the marsh at which birds can see far enough back over the vegetation to reliably detect an approaching raptor. This distance would vary with the height of the vegetation, the birds' head-up height and the raptor's altitude and approach velocity. We can only speculate on the critical distance here because our measures of location were rather coarse. However, because birds in strip 1 were highly likely to fly or to look up, whereas birds in the second strip tended only to look up, the critical distance for *Calidris* at this site may be ca. 1 m from the marsh. Birds closer than that tend to fly but those farther away tend only to look up, and if a predator is seen, would then undoubtedly fly away. Indeed, naturally occurring appearances of harriers during the study led to all birds in the area taking flight.

Finally, it should be noted that the behavior described above is not restricted to avocet alarm calls, nor to alarm calls at all. Throughout the course of the study many "fly-ups" were observed in response to calls by Willets (*Catoptrophorus semipalmatus*), Marbled Godwits (*Limosa fedoa*), and Killdeer (*Charadrius vociferus*), as well as *Limnodromus* and *Calidris* species. In addition, before conducting this study, Leger observed that *Calidris* sandpipers nearest the marsh were far more likely to fly in response to a single handclap than ones farther from the marsh (but closer to the sound source). Clearly, the marsh seems to be a potent determinant of shorebird behavior.

SUMMARY

Following playbacks of an American Avocet alarm-call recording, *Calidris* sandpipers foraging on a mudflat either flew away from the nearby marsh vegetation, looked up without flying, or continued foraging. The probability of flying and of looking up was highest in birds closest to the marsh, even though they were farthest from the playback speaker. The results

suggest that sandpipers assess their distance from the predator-concealing marsh vegetation and modify their behavior accordingly. Thus, contextual information and information in the alarm call jointly affect sandpiper behavior.

ACKNOWLEDGMENTS

This research was funded through a grant to Leger from the Chancellor's Patent Fund at the University of California, Davis (#3–444080–08613–5). We thank Ted Chandik and Lawrence White of the Parks and Open Space Management Office of the City of Palo Alto, California, for permission to work at the Baylands Nature Center. Edward H. Miller provided many helpful comments on an earlier version of the manuscript.

LITERATURE CITED

Caraco, T., S. Martindale and H. R. Pulliam. 1980. Avian time budgets and distance to cover. Auk 97:872–875.

Charnov, E. L. and J. R. Krebs. 1975. The evolution of alarm calls: altruism or manipulation? Am. Nat. 109:107–112.

Dekker, D. 1980. Hunting success rates, foraging habits, and prey selection of Peregrine Falcons migrating through central Alberta. Can. Field-Nat. 94:371–382.

Hodgdon, H. E. and J. S. Larson. 1973. Some sexual differences in behaviour within a colony of marked beavers (*Castor canadensis*). Anim. Behav. 21:147–152.

Hunt, W. G., R. R. Rogers and D. J. Slowe. 1975. Migratory and foraging behavior of Peregrine Falcons on the Texas coast. Can. Field-Nat. 89:111–123.

Kirk, R. E. 1968. Experimental design: procedures for the behavioral sciences. Brooks/Cole, Belmont, California.

Leger, D. W. and D. H. Owings. 1978. Responses to alarm calls by California ground squirrels: effects of call structure and maternal status. Behav. Ecol. Sociobiol. 3:177–186.

———, ——— and L. Boal. 1979. Contextual information and differential responses to alarm whistles in California ground squirrels. Z. Tierpsychol. 49:142–155.

———, ——— and D. L. Gelfand. 1980. Single-note vocalizations of California ground squirrels: graded signals and situation-specificity of predator and socially evoked calls. Z. Tierpsychol. 52:227–246.

Noyes, D. H. and W. G. Holmes. 1979. Behavioral responses of free-living hoary marmots to a model golden eagle. J. Mammal. 60:408–411.

Owens, N. W. and J. D. Goss-Custard. 1976. The adaptive significance of alarm calls given by shorebirds on their winter feeding grounds. Evolution 30:397–398.

Owings, D. H. and D. W. Leger. 1980. Chatter vocalizations of California ground squirrels: predator- and social-role specificity. Z. Tierpsychol. 54:163–184.

Page, G. and D. F. Whitacre. 1975. Raptor predation on wintering shorebirds. Condor 77:73–83.

Recher, H. F. 1966. Some aspects of the ecology of migrant shorebirds. Ecology 47:393–407.

Rudebeck, G. 1950. The choice of prey and modes of hunting of predatory birds with special reference to their selective effect. Oikos 2:66–88.

———. 1951. The choice of prey and modes of hunting of predatory birds with special reference to their selective effect. Oikos 3:200–231.

Seyfarth, R. M., D. L. Cheney and P. Marler. 1980a. Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. Science 210:801–803.

———, ——— AND ———. 1980b. Vervet monkey alarm calls: semantic communication in a free-ranging primate. Anim. Behav. 28:1070–1094.

SMITH, W. J. 1965. Message, meaning and context in ethology. Am. Nat. 99:405–409.

———. 1977. The behavior of communicating: an ethological approach. Harvard Univ. Press, Cambridge, Massachusetts.

WILSON, E. O. 1975. Sociobiology: the new synthesis. Belknap/Harvard Univ. Press, Cambridge, Massachusetts.

DEPT. PSYCHOLOGY, UNIV. NEBRASKA, LINCOLN, NEBRASKA 68588–0308.
ACCEPTED 15 OCT. 1981.

Wilson Bull., 94(3), 1982, pp. 329–337

NEST-SITE SELECTION BY CAVITY-NESTING BIRDS OF RIPARIAN HABITATS IN IOWA

Dean F. Stauffer and Louis B. Best

Nest-site selection is an important component of habitat selection by birds (Hildén 1965). Nest-sites selected by a species should represent the cumulative effects of evolutionary pressures that have maximized reproductive success (Caccamise 1977). Competition for nest-sites may be rigorous among cavity-nesting species (von Haartman 1957, Franzreb 1976) and may limit the availability of sites suitable for nesting.

Although considerable effort has been expended to study interspecific relationships within avian communities, little research has been devoted to the analysis of nest-site selection at the community level. Beecher (1942) provided a general description of nest-site selection within a community. Preston (1946), Preston and Norris (1947), Cruickshank (1956), Taylor (1965), and DeGraff et al. (1975) have reported on nest heights selected by birds in various habitats, but they did not provide supplemental nest-site measurements. More recently, Conner and Adkisson (1977), studying five woodpecker (Picidae) species, and McCrimmon (1978), studying five heron (Ardeidae) species, have conducted principal component analysis on several nest-site measurements.

In view of the general lack of information on nest-site selection at the community level, particularly for cavity-nesting species, the objective of this paper is to describe the interrelationships among nest-sites chosen by cavity-nesting species of riparian communities (herein defined as uncultivated land within 250 m of the stream edge).

STUDY AREA AND METHODS

Twenty-eight sites were selected for study in southeastern Guthrie County, Iowa, along Brushy Creek, Beaver Creek, and the Middle and South Raccoon rivers. In choosing study sites, an effort was made to sample a broad spectrum of riparian habitats. A total of 142 ha comprising six general habitat types was sampled. Characteristics of the six types (herbaceous, 8.9 ha; savannah, 5.5 ha; scrub, 3.8 ha; wooded edge, 6.8 ha; floodplain woodland, 28.4 ha; and upland woodland, 88.8 ha) and the study area in general are detailed in Stauffer and Best (1980).

Fieldwork was done mid-April through mid-July in 1976 and 1977 as part of an avian community study (Stauffer and Best 1980). Some nests were found during early morning breeding-bird censuses of the study sites, but most were located after censuses and during evening hours by watching nesting behavior and systematically searching suitable areas. We attempted to locate nests of every cavity-nesting species present on each study site. The sample is biased, however, because nests located in more open sites where birds could be followed more easily were represented disproportionately.

The following measurements were recorded for each cavity nest located: nest height and height of supporting substrate, relative nest height (nest height/support height), limb (trunk) diameter and angle from horizontal at the nest cavity, and compass orientation of the nest-cavity entrance. The date of nest initiation either was determined by direct observation of nest building or was estimated by backdating from the time when young were observed being fed.

Before statistical operations were performed, the data were checked for normality. The variables nest height, support-structure height, and supporting limb (trunk) diameter were found not to be normal and were transformed by using natural logarithms, resulting in more normal distributions. Mean values and Pearson product-moment correlations among the variables were calculated for primary (i.e., cavity-excavating) and secondary cavity nesters. A direct discriminant function analysis (Nie et al. 1975) was used to compare interrelationships of the species' nest-sites on the basis of the measured variables.

RESULTS AND DISCUSSION

Univariate analysis.—In general, nests of primary cavity nesters (PCN) were higher ($\bar{x}$ = 8.3 m) than those of secondary cavity nesters (SCN, $\bar{x}$ = 6.2 m) (Table 1). Nest height differences were statistically significant among PCN and among SCN as well as between the two groups of species (Table 2). Similar trends were evident in support-structure height (Tables 1, 2). Nest and support-structure heights were more variable for SCN than for PCN (as indicated by higher F values, Table 2) and were weakly correlated with the date of nest initiation in the former (Table 3). The greater variation in nest-sites of SCN may be because, as a whole, these species have fewer options in their choice of nest-sites and must choose from those abandoned by PCN or that occur naturally.

Although relative nest height differed significantly among SCN (Table 2), it was quite consistent among PCN. Nests of all cavity nesters, however, were placed relatively lower in tall than in short support structures (Table 3), probably because taller snags (standing dead trees) have smaller limbs on top that are unsuitable for nesting. Shorter snags generally are older and in more advanced stages of decay; consequently, their smaller branches more likely would have been broken off.

Limb (trunk) diameter at the nest cavity differed significantly for all comparisons made (Table 2). PCN selected larger limbs (trunks) for nest support ($\bar{x}$ = 26.0 cm) than did SCN ($\bar{x}$ = 21.6 cm) (Table 1), suggesting that not all cavities abandoned by PCN are preferred equally by SCN. (Approximately 20–30% of SCN nests were in natural cavities, which, in part, may explain the difference between PCN and SCN nest-sites.) The negative correlation of supporting limb diameter with date of nest initiation for each group (Table 3) probably resulted from Downy Woodpeckers (see Table 1 for scientific names) and House Wrens nesting relatively late in the breeding season. These species selected relatively small-diameter limbs (trunks) for nest support (Table 1).

TABLE 1
MEANS AND STANDARD DEVIATIONS OF SELECTED VARIABLES MEASURED AT 298 CAVITY NESTS

Species	Sample size	Nest height (m)	Support-structure height (m)	Limb (trunk) diameter at cavity (cm)	Supporting limb (trunk) angle (°)[a]
Primary cavity nesters	134	8.3 ± 3.7	13.6 ± 6.3	26.0 ± 10.5	69.7 ± 19.6
Common Flicker (*Colaptes auratus*)	31	8.1 ± 3.2	14.9 ± 6.6	34.5 ± 10.6	73.7 ± 17.1
Red-bellied Woodpecker (*Melanerpes carolinus*)	14	8.4 ± 2.7	13.6 ± 7.4	26.7 ± 5.9	63.6 ± 23.1
Red-headed Woodpecker (*M. erythrocephalus*)	59	9.6 ± 3.7	14.6 ± 5.7	25.7 ± 9.3	69.8 ± 18.5
Downy Woodpecker (*Picoides pubescens*)	30	6.1 ± 3.1	10.2 ± 5.6	18.8 ± 6.0	68.0 ± 22.4
Secondary cavity nesters	164	6.2 ± 4.0	10.5 ± 7.4	21.6 ± 8.9	61.3 ± 23.7
Great Crested Flycatcher (*Myiarchus crinitus*)	13	8.5 ± 3.3	16.9 ± 7.0	24.7 ± 11.1	62.7 ± 27.0
Black-capped Chickadee (*Parus atricapillus*)	25	2.2 ± 2.1	4.0 ± 5.2	20.3 ± 7.8	73.6 ± 21.7
White-breasted Nuthatch (*Sitta carolinensis*)	9	7.2 ± 3.1	17.8 ± 7.9	33.2 ± 13.1	55.0 ± 28.1
House Wren (*Troglodytes aedon*)	82	5.4 ± 2.9	8.4 ± 5.0	19.6 ± 7.1	60.8 ± 23.0
Starling (*Sturnus vulgaris*)	22	9.7 ± 4.5	15.5 ± 7.8	25.9 ± 9.9	62.5 ± 16.8
House Sparrow (*Passer domesticus*)	13	10.7 ± 3.8	16.4 ± 6.3	18.5 ± 5.1	39.6 ± 27.2

[a] Angle measured from horizontal.

Limb angle at the nest cavity was not different among primary cavity-nesting species (PCNS), but differed significantly among secondary cavity-nesting species (SCNS) and between the two groups (Table 2). The negative correlations of limb angle with nest and support-structure heights for SCN (Table 3) probably is because higher nests were placed in branches that lean more away from the main trunk, whereas lower nests usually were found in snags in advanced stages of decay with only the trunk and the bases of main branches remaining.

Compass orientation of entrances to cavity nests has been found to be nonrandom for several cavity-nesting species (Lawrence 1967, Dennis 1969, Reller 1972, Conner 1975). Nest cavities often are oriented to the south

Table 2

F-statistics from One-way ANOVA's of Differences Among Species and Between Groups of Species in the Variables Measured at Cavity Nests

Variable	All cavity nesters (df = 9, 289)	Primary cavity nesters (df = 3, 130)	Secondary cavity nesters (df = 5, 158)	Primary vs secondary cavity nesters (df = 1, 296)
Nest height	23.66***	6.71***	26.26***	28.15***
Support-structure height	23.35***	6.00***	24.92***	26.14***
Relative nest height	2.32*	1.10	3.59**	0.23
Supporting limb (trunk) diameter	8.19***	10.86***	5.63***	8.43**
Supporting limb (trunk) angle	3.95***	0.96	3.86***	10.71**

* $P \leq 0.05$; ** $P \leq 0.01$; and *** $P \leq 0.001$.

and east, which may allow sunlight to warm the nest or permit nest ventilation by prevailing winds (Conner 1975). In our study, there was no consistent pattern in woodpecker nest orientation, although nest orientation was statistically nonrandom for PCN (Table 4). Of the 133 primary cavity nests, 94% were located on the underside of sloping limbs (trunks). Thus, birds may be choosing nest-sites primarily on the basis of limb (trunk) angle, and nest-entrance orientation may be only an indirect consequence of the former (see Conner 1975).

Table 3

Correlations Between Variables Measured at Primary (N = 134) and Secondary (N = 164) Cavity Nest-sites[a]

Variable	Cavity-nest type	NID	NH	SSH	RNH	SLD	SLA
Nest-initiation date	Primary	1.0					
	Secondary	1.0					
Nest height	Primary	0.11	1.0				
	Secondary	0.22	1.0				
Support-structure height	Primary	0.11	0.70	1.0			
	Secondary	0.21	0.90	1.0			
Relative nest height	Primary	−0.01	0.29	−0.46	1.0		
	Secondary	−0.04	−0.05	−0.47	1.0		
Supporting limb (trunk) diameter	Primary	−0.16	0.10	−0.01	0.07	1.0	
	Secondary	−0.28	0.05	0.12	−0.21	1.0	
Supporting limb (trunk) angle	Primary	−0.15	0.09	−0.02	0.14	0.38	1.0
	Secondary	−0.12	−0.12	−0.15	0.12	0.07	1.0

[a] Significant ($P \leq 0.05$) correlation values are 0.14 and 0.13 for primary and secondary cavity nest-sites, respectively.

TABLE 4
NEST-ENTRANCE ORIENTATION RELATIVE TO THE CENTER OF THE NEST-SUPPORT STRUCTURE FOR CAVITY-NESTING SPECIES

Orientation	Percent of nests	
	Primary cavity nesters	Secondary cavity nesters
N	16	14
NE	9	15
E	20	15
SE	6	12
S	14	15
SW	10	8
W	16	10
NW	9	11
Total nests	133	157
Chi-square value	16.1	6.5
Significance level	<0.05	>0.50

On the basis of similarities in woodpecker and Eastern Bluebird (*Sialia sialis*) nest-entrance orientation, Pinkowski (1976) concluded that bluebirds randomly selected nest-sites, most of which were woodpecker cavities. Nest-entrance orientation in our study did not differ between PCN

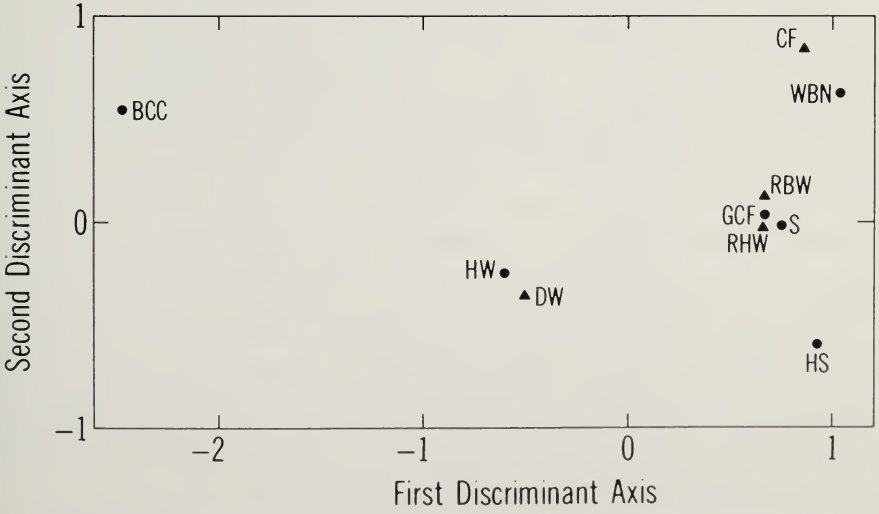


FIG. 1. Two dimensional ordination for nest-sites of 10 cavity-nesting species using the first and second discriminant axes. Species' codes are in Table 1.

and SCN ($\chi^2 = 8.99$, df = 7, $P > 0.10$), seemingly supporting the notion that nest-site selection by SCN is random. Significant differences between PCN and SCN in four of five nest-site measurements, however, suggest that SCN may not randomly select woodpecker cavities even though orientation of the nest-cavity entrances is similar. The apparent paradox may be explained by the fact that snags are continually decomposing; thus, characteristics of a nest-site excavated by a woodpecker may change by the time that the same site is used by a SCN.

Multivariate analysis.—To determine the degree of dissimilarity among nest-sites of the 10 cavity-nesting species, a discriminant analysis was conducted using five variables (Table 5). (This was done after the results from a MANOVA of the five variables proved statistically significant.) The species' mean discriminant values then were ordinated on the first two discriminant axes (Fig. 1). Support-structure height loaded most heavily in the first function derived (Table 5). The ordination of nest-sites on the first axis separated only three species (Black-capped Chickadee, House Wren, and Downy Woodpecker) from the others (Fig. 1); all three species chose smaller trees or snags for nesting. The second function further discriminated species primarily on the basis of nest height and supporting limb (trunk) diameter. Values along the resultant axis (Fig. 1) increase as nest height decreases and as supporting limb (trunk) diameter increases. White-breasted Nuthatches and Common Flickers, which nested low in larger structures, and House Sparrows, which nested high in smaller structures, were well separated from the main group on the second axis.

Starlings, Great Crested Flycatchers, and Red-headed and Red-bellied woodpeckers chose notably similar nest-sites on the basis of the five variables used (Fig. 1). This suggests a potential for considerable nest-site competition among these four species, although including additional variables in the analysis might have resulted in better separation. Great Crested Flycatchers nest more often in dead limbs of live trees and in live trees than do the other three species (Stauffer and Best 1980). Thus, although flycatchers select nest-sites structurally similar to those of the other species, the potential for competition may be low. Although Red-headed and Red-bellied woodpeckers choose similar nest-sites, they may avoid competition by selecting different habitats and (or) nesting at different times (Jackson 1976). Starlings have an extended breeding season (Collins and de Vos 1966) and occupy a variety of habitats; thus, they are potential competitors for nest-sites with the other three species (see also Erskine and McLaren 1976, Troetschler 1976, Short 1979). Once, two Starlings were observed taking over an active Red-headed Woodpecker nest.

PCN and SCN were discriminated principally on the basis of support-structure height (Table 5). The other four variables were relatively unim-

TABLE 5

SUMMARY OF DIRECT DISCRIMINANT ANALYSES CONDUCTED ON NEST-SITES OF CAVITY-NESTING SPECIES[a]

Variable	Standardized coefficients of the first two functions[b]						
	All cavity nesters		Primary cavity nesters		Secondary cavity nesters		Primary vs. secondary cavity nesters
	I	II	I	II	I	II	I[c]
Nest height	−0.127	−0.660	−2.379	−1.306	1.566	−1.064	−0.658
Support-structure height	1.194	0.414	3.305	2.023	−0.722	1.398	1.634
Relative nest height	0.457	0.004	2.243	1.924	−0.608	1.220	0.671
Supporting limb (trunk) diameter	0.445	0.717	0.976	−0.491	0.305	−0.646	0.291
Supporting limb (trunk) angle	−0.205	0.447	−0.264	−0.083	−0.265	−0.507	0.466
Cumulative variance accounted for	72.9	88.1	81.1	96.5	76.8	91.2	100.00

[a] Analyses were run among all cavity-nesting species, among primary cavity-nesting species, among secondary cavity-nesting species, and between primary and secondary cavity nesters.
[b] All functions presented are significant ($P < 0.05$), as determined by minimization of Wilk's lambda.
[c] Only one function can be derived when only two groupings are being discriminated.

portant in distinguishing between the two guilds. Significant discrimination between the two guilds on the basis of five variables indicates that SCN have selective preferences among the available cavities abandoned by woodpeckers.

The first discriminant function of an analysis among PCNS weighted heavily on support-structure height and somewhat less on nest and relative nest heights (Table 5). (Because relative positions of both PCNS and SCNS when plotted separately on their first two discriminant axes were similar to those in Fig. 1, they are not presented here.) The second function further separated PCNS that were similar for the first function on the basis of support-structure height and relative nest height. Thus, PCNS seem to be partitioning nest-sites mainly on the basis of substrate structure size. Conner and Adkisson (1977), using principal component analysis, were able to define a gradient for nest-sites of five woodpecker species on the basis of nest-tree diameter.

The most important variable derived in the first function that discriminated among SCNS was nest height (Table 5). The second function was dominated by support-structure and relative nest heights. Except for Starlings and Great Crested Flycatchers, the discriminant analysis separated SCNS well.

Patterns of nest-site selection for PCN and SCN differ. Woodpeckers partition nest-sites primarily on the basis of substrate height, whereas SCN mainly choose nest-sites on the basis of cavity height and secondarily by support-structure height.

SUMMARY

Nest-site selection by 10 cavity-nesting species was analyzed on the basis of five nest-site variables. Discriminant analysis showed considerable separation among nest-sites for 6 of the 10 species, mainly on the basis of nest substrate size. The other four species potentially compete for nest-sites. When analyzed separately, primary cavity nesters and secondary cavity nesters exhibited different patterns in nest-site partitioning. Woodpecker species chose different nest-sites mainly on the basis of support-structure height, whereas secondary cavity nesters primarily segregated nest-sites on the basis of cavity height.

Differences in four of the five variables and results of discriminant analysis suggest that SCN were not randomly choosing cavities abandoned by woodpeckers.

ACKNOWLEDGMENTS

Thomas Rosburg and Robert Deitchler assisted in collecting field data, and LeRoy Wolins helped in the statistical analyses. Reviews of an earlier draft by Robert Whitmore and Nancy Flood are appreciated. This project was funded by the U.S. Fish and Wildlife Service, Office of Biological Services, National Stream Alteration Team; administered through the Cooperative Wildlife Research Unit, Iowa State University, Ames. Journal Paper No. J-10012 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project No. 2085.

LITERATURE CITED

Beecher, W. J. 1942. Nesting birds and the vegetation substrate. Chicago Ornithol. Soc., Chicago, Illinois.

Caccamise, D. F. 1977. Breeding success and nest site characteristics of the Red-winged Blackbird. Wilson Bull. 89:396–403.

Collins, V. B. and A. de Vos. 1966. A nesting study of the Starling near Guelph, Ontario. Auk 83:623–636.

Conner, R. N. 1975. Orientation of entrances to woodpecker nest cavities. Auk 92:371–374.

——— and C. S. Adkisson. 1977. Principal component analysis of woodpecker nesting habitat. Wilson Bull. 89:122–129.

Cruickshank, A. D. 1956. Nesting heights of some woodland warblers in Maine. Wilson Bull. 68:157.

DeGraff, R. M., H. R. Pywell, and J. W. Thomas. 1975. Relationships between nest height, vegetation and housing density in New England suburbs. Trans. Northeast Sect. Wildl. Soc. 32:130–150.

Dennis, J. V. 1969. The Yellow-shafted Flicker (*Colaptes auratus*) on Nantucket Island, Massachusetts. Bird-Banding 40:290–308.

Erskine, A. J. and W. D. McLaren. 1976. Comparative nesting biology of some hole-nesting birds in the Cariboo Parklands, British Columbia. Wilson Bull. 88:611–620.

Franzreb, K. E. 1976. Nest site competition between Mountain Chickadees and Violet-green Swallows. Auk 93:836–837.

Hildén, O. 1965. Habitat selection in birds. Ann. Zool. Fenn. 2:53–75.

Jackson, J. A. 1976. A comparison of some aspects of the breeding ecology of Red-headed and Red-bellied woodpeckers. Condor 78:67–76.

Lawrence, L. de K. 1967. A comparative life-history of four species of woodpeckers. Ornithol. Monogr. 5.

McCrimmon, D. A., Jr. 1978. Nest site characteristics among five species of herons on the North Carolina coast. Auk 95:267–280.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. Statistical package for the social sciences. McGraw-Hill, Inc.

Pinkowski, B. C. 1976. Use of tree cavities by nesting Eastern Bluebirds. J. Wildl. Manage. 40:556–563.

Preston, F. W. 1946. Nesting heights of birds building in shrubs. Ecology 27:87–91.

——— and R. T. Norris. 1947. Nesting heights of breeding birds. Ecology 28:241–273.

Reller, A. W. 1972. Aspects of behavioral ecology of the Red-headed and Red-bellied woodpeckers. Am. Midl. Nat. 88:270–290.

Short, L. L. 1979. Burdens of the picid hole-excavating habit. Wilson Bull. 91:16–28.

Stauffer, D. F. and L. B. Best. 1980. Habitat selection by birds of riparian communities: evaluating effects of habitat alterations. J. Wildl. Manage. 44:1–15.

Taylor, W. K. 1965. Nesting heights of some Louisiana birds. Wilson Bull. 77:146–150.

Troetschler, R. G. 1976. Acorn woodpecker breeding strategy as affected by Starling nest-hole competition. Condor 78:151–165.

von Haartman, L. 1957. Adaptation in hole-nesting birds. Evolution 11:339–347.

DEPT. ANIMAL ECOLOGY, IOWA STATE UNIV., AMES, IOWA 50011. (PRESENT ADDRESS DFS: DEPT. WILDL. RESOUR., UNIV. IDAHO, MOSCOW, IDAHO 83843.) ACCEPTED 15 DEC. 1981.

Wilson Bull., 94(3), 1982, pp. 338–349

NESTS, TERRITORIES, AND REPRODUCTION OF SEDGE WRENS (*CISTOTHORUS PLATENSIS*)

JEFFREY T. BURNS

Sedge Wrens (*Cistothorus platensis*) share many features of their breeding biology with the congeneric Marsh Wren (*C. palustris*). Both species defend all-purpose territories in "grassland" habitat (Orians 1969), are highly insectivorous, and while sexually monomorphic in appearance, populations of both species may exhibit polygyny at levels ranging from 30–50% (Welter 1935; Walkinshaw 1935; Verner 1964, 1965a; Kale 1965; Crawford 1977). Males of both species build a number of domed nests which play a central role in courtship (Verner 1965a, Burns 1977). Crawford (1977) has documented the occurrence of polygyny in the Sedge Wren, but few other basic features of the social organization of this species have been reported, thus precluding valuable comparisons with the better studied Marsh Wren. This paper discusses territory characteristics, reproductive performance, parental care and mating patterns of Sedge Wrens.

STUDY AREA

The 3.3-ha study site is located in Polk County, Minnesota, 20 km east and 10 km south of Crookston. The sedge meadow used by the wrens during the 1976 season was subject to light grazing by cattle as recently as 1973, but in 1976 it appeared relatively undisturbed. Grasses (*Calamogrostis neglecta*, *C. inexpansa*) and sedges (*Scirpus acutis*, *Carex stricta*, *C. sartwellii*, *C. buxbaumii*, *C. aquatilis*) were the most abundant species. The meadow was flooded with about 20 cm of water early in May but by late July no standing water was present. Yellow Warblers (*Dendroica petechia*), Yellowthroats (*Geothylpis trichas*), Red-winged Blackbirds (*Agelaius phoeniceus*) and Swamp Sparrows (*Melospiza georgiana*) were also common in the meadow.

METHODS

Twelve males and 14 females were captured for banding by chasing them into mist nets placed in their territories and near nests. Sexes were distinguished by song and by the presence or absence of a cloacal protuberance (Salt 1954). Five males situated near observation towers ("tower males") were individually color banded; 12 of the 14 females were color banded by the time their first young fledged. Observations were made using binoculars and a spotting telescope from three 2-m high open towers and from canvas blinds located near nests. Observations were made almost daily from 12 May–11 August 1976. Watches from the towers began before sunrise and continued until males began foraging at about 07:30 (CST). Evening watches extended from about 19:00 until activity ceased after sunset. A 25-m grid of lathing helped to pinpoint male singing locations and was used to estimate territory size.

Data on parental care and foraging patterns were collected from blinds during the periods 07:30–12:00 and 16:00–20:00 in June, 09:00–12:00 and 16:00–19:00 in July and August. After

arriving in the first blind I waited 5 min for the birds to settle down and then collected data on the first 15 trips by the female. I then moved to another blind and so sampled the activities at three or four nests each morning and evening, rotating the order of observation from day-to-day. Data collected at 14 nests included: (1) distance from the nest to where foraging began, (2) kind of vegetation used for foraging, (3) whether or not the site was within the male's territory, and (4) the length of time spent at and away from the nest. Rarely could I identify what the young were being fed.

Nests were examined at least every second day. Those found during incubation were back-dated based on a 14-day incubation period (Walkinshaw 1935, Crawford 1977). Three nests were found after the young had hatched and were dated by comparing the degree of development with young of known age. Nests were located either by observing males building them or by systematic searches using a stick to brush aside the concealing vegetation. Territories were searched for nests at least once a week.

Pair bond terminology follows Martin (1974). The first female to pair with a polygynous male is a "primary" female, while subsequent mates, regardless of the extent of temporal overlap with first paired females, are "secondary" females. Nests with eggs laid in them before 1 July are "early nests"; those begun afterwards are "late nests."

RESULTS

The multiple nests built by *Cistothorus* males are used for nesting, as dormitories, and possibly as decoys for predators (Verner 1965a, Burns 1977). Those used for nesting have a substantial inner lining of grass, sedge and feathers added by females. Most courtship activities occur near nests; Verner and Engelson (1970) found a positive relationship between the number of nests built by male Marsh Wrens and the number of females to whom they were mated. The 12 male Sedge Wrens on my study area built an average of 7.4 complete nests per male (Table 1) from 17 May–11 August. Males were still building when I left in August, and since four males left in late July while the remaining males continued to build nests, I estimate that males present for the entire season build an average of about nine nests. Males left an average of 0.8 nests incomplete, consisting of only a spheroid network of sedge or grass. There were no instances of stacked nests (one built on top of another) nor of nests built in localized "courting centers" (Fig. 1), both of which have been reported for Marsh Wrens (Verner 1965a, Verner and Engelson 1970).

I found no significant relationship (Spearman Rank Correlation) between the number of nests built in each territory and (a) territory size, or (b) amounts of the major vegetation types (*Scirpus acutis*, *Carex stricta*, *C. aquatilis*). Polygynous males built eight, seven, and seven nests each, suggesting no clear relationship between the ability to attract second mates and the number of nests built. The sample sizes are too small, however, to support conclusions in this regard.

Territory size.—Sedge Wren territories are used for courting, nesting and much of the foraging. The territories presented in Fig. 1 represent

Table 1

Territory Size, Composition and Number of Nests Built by 12 Male Sedge Wrens

Male	Territory size (m^2)[a]	Amount major vegetation (m^2)[b]	% major vegetation	No. of nests
B	1589	1225	82	8
R	1274	970	76	8
G	1777	1402	79	5
Y	1486	853	57	9
BB	2106	1580	75	8
M54	1592	902	57	13
M62	1844	1242	70	7
M63	3559	501	14	5
M66	1287	597	46	6
M67	1586	1008	63	6
M69	1570	615	39	7
M71	1695	1057	62	7
$\bar{x}$	1780	996	60	7.4

[a] Based on territories of the week 9 July–15 July.
[b] Major vegetation includes *Scirpus acutis-Carex stricta-C. aquatilis*, and monotypic patches of *C. aquatilis*.

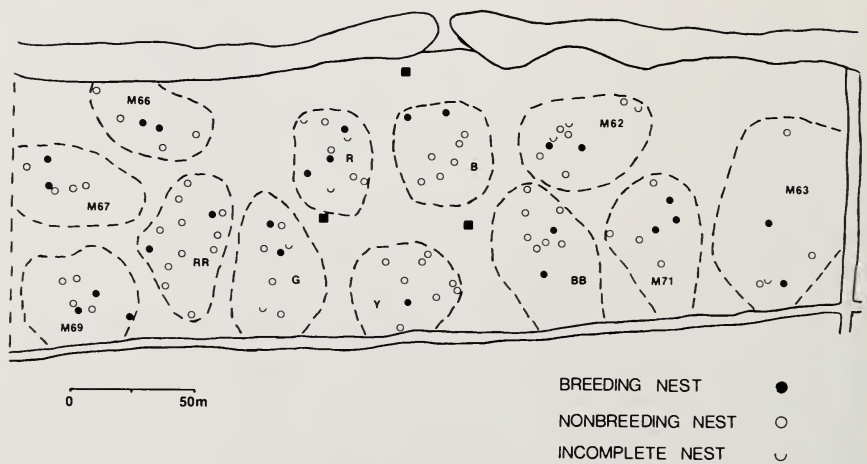


Fig. 1. Territories of 12 male Sedge Wrens during the week beginning 9 July, when most females were beginning their second clutches.

"maximum" areas of males (Odum and Kuenzler 1955, Stenger and Falls 1959), determined by plotting the positions of males while singing during the week beginning 9 July and taking the largest perimeter. All new positions were recorded, rather than plotting positions at constant intervals (Odum and Kuenzler 1955) or at each sighting (Stenger and Falls 1959). The average territory size of the 12 males was 1780 m^2 (Table 1). Territory sizes of the five tower males were estimated separately for 8 consecutive weeks, based on about 20 h of observation per week. Seasonal maximum territories were constructed by superimposing the eight weekly estimates for each male and taking the largest perimeter, yielding an average seasonal maximum territory size of 2259 m^2. The grand mean, 1280 m^2, an average of the 40 estimates obtained for the five males, is considerably less than that obtained by superimposing the weekly territories. Thus, males tended to stop defending some portions of their territories and shifted to new areas as the season progressed.

Reproduction.—Females began laying on or about the third day of nestlining, after which one egg was laid each day. Incubation began before clutches were complete, as hatching extended over a 2- or 3-day period. Only females incubated. The incubation period, from the laying of the last egg to hatching of the last egg, was normally 14 days (six of seven nests with all eggs hatching). The overall nesting success (number of nests producing at least one young/number of initiated clutches) was high (69%), as expected for a passerine species laying in an enclosed nest (Nice 1957), and was similar to that reported by Crawford (1977) for a sample of 31 nests (68%). Nest failures in my study were due to predation (five) or infertile clutches (two). One of the five nests whose contents were thought to have been preyed on may instead have been destroyed by another wren (see Picman 1977a, 1977b).

Apparently females in some populations of Sedge Wrens are double-brooded (a second clutch of eggs is produced after young from the first nest fledge), whereas females in other populations are not. Walkinshaw (1935) suggested that Sedge Wrens are double-brooded, based on records of very late nesting dates, whereas Crawford (1977) found that none of the females he studied renested after producing young. In the population I studied most of the successful females laid additional clutches (Fig. 2), but with interesting exceptions. Three of the 12 males were paired to two different females during the season. In two of these cases the primary female did not renest, while in the third case the female did renest but after pairing to a male on a different territory. Monogamous and primary females began their nests within a week of each other, on the average, while primary and secondary females differed by about one and a half months. Late nests of previously successful monogamous females were begun at nearly the same time as were the first nests of secondary females.

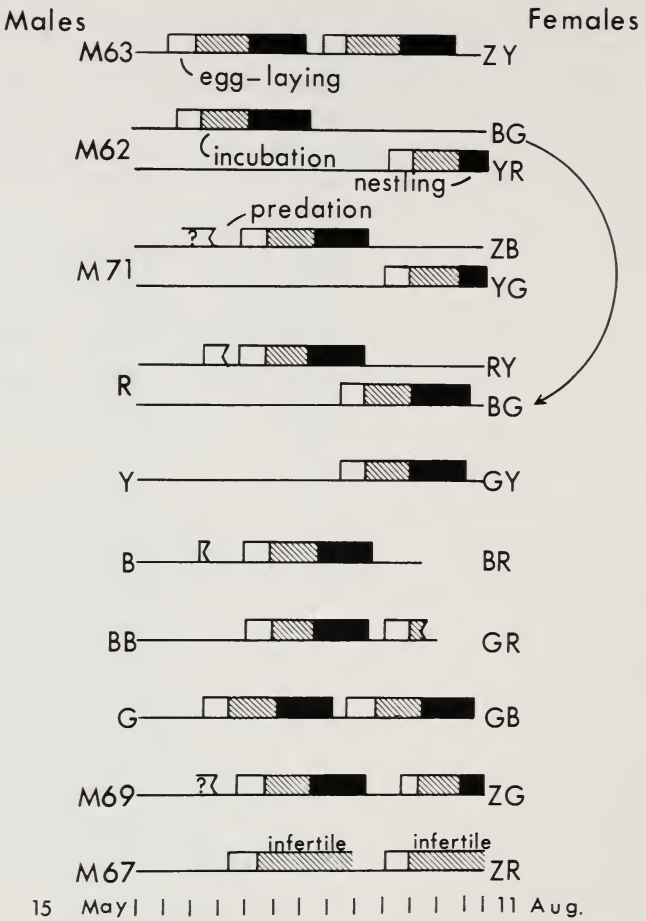


FIG. 2. Nesting schedule of Sedge Wrens over weekly intervals. Clutch initiation dates for two destroyed nests are unknown and are indicated by question marks. The reproductive activities in one other territory were similar to those shown for BB's territory, while events in a second unrepresented territory resembled those in M63's.

All first clutches of monogamous and primary females found prior to hatching contained seven eggs (Table 2), the clutch-size suggested by Bent (1948). Clutch-sizes of late nests of monogamous females were more variable (4–7) and were significantly smaller than first clutches ($t = 4.54$, $P < 0.001$). Secondary females laid slightly larger clutches ($\bar{x} = 6.0$) than did late nesting monogamous females ($\bar{x} = 5.7$), but the sample sizes are small. Monogamous females fledged significantly fewer young late in the season than they did earlier ($t = 6.06$, $P < 0.001$) and about the same

TABLE 2
CLUTCH-SIZE AND FLEDGING SUCCESS OF EARLY[a] AND LATE NESTING FEMALE SEDGE WRENS

Pairing status	Clutch-size		Young produced		Fledging success	
	Early	Late	Early	Late	Early	Late
Monogamous	7.0 (5)[b]	5.7 (8)	5.1 (6)	3.4 (5)	0.72 (6)	0.56 (5)
Primary	7.0 (2)	—	5.3 (3)	—	0.75 (3)	—
Secondary	—	6.0 (3)	—	3.3 (3)	—	0.55 (3)

[a] Early nests were those initiated before 1 July 1976.
[b] Sample sizes are in parentheses.

number as did secondary females nesting at the same time (Table 2). Overall, the fledging success (number of young fledged per number of eggs laid, including only nests from which at least one young fledged) was 0.67, but again seasonal differences occurred. Early nests of monogamous females averaged 0.72 young per egg laid, while late in the season these same females fledged 0.56 young per egg laid. Secondary females had a fledging success of 0.55 young per egg laid.

Average differences between the reproductive success of monogamous and polygynous males were the result of a higher rate of nest failure for monogamous males. Monogamous males produced an average of 5.9 young during the season, while polygynous males averaged 8.6 young. This difference resulted largely from predation on the late nests of monogamous males and the two infertile clutches of M67. If only monogamous males that successfully produced young from both early and late nests are considered, monogamous males average 8.5 young (N = 4).

Parental care.—Table 3, based on 98 h of observation at 14 nests, summarizes feeding schedules for 1976. All but three nests were observed from at least day 4 to day 10 (average nestling age; day of hatching is day 0). Most males continued to advertize for females and build nests during the nestling period, and consequently provided little food for nestlings. While six of the nine males observed were recorded bringing food to nestlings, only three males contributed 10% or more of the nestlings' food (based on number of trips). The extent of male parental care was similar for first and second broods of monogamous females and for the single broods of primary and secondary females. There did not appear to be a correlation between the number of young fledged and the extent of male parental care.

As with Marsh Wrens and other passerine species (Verner 1965a, Royama 1966, Martin 1974) Sedge Wrens tend to feed nestlings more fre-

Table 3
Provisioning of Nestlings by Adult Sedge Wrens

Male	Female	Total trips	Trips by male	Young fledged
R	RY (early)	187	2	6
	BG (late)	141	1	3
M71	ZB (early)	51	18	6
	YG (late)	89	0	4
M62	BG (early)	71	11	4
	YR (late)	58	13	3
G	GB (early)	163	0	5
	GB (late)[a]	154	0	4
M64	ZG (early)	110	0	6
	ZG (late)	33	0	3
Y	GY (late)	193	86	3
BB	GR (early)	102	0	5
M54	RG (early)	107	10	5
M66	YB (early)	52	3	4
Total		1511	144	

[a] Male G disappeared after female GB completed laying her second clutch.

quently as the nestlings age. Females also fed similarly-aged young at significantly higher rates later in the season than earlier (Wilcoxon Ranked Pairs Sign Test, $P < 0.01$), as Gibb (1950) also found for two species of parids. No clear tendency for males to increase their feeding rates was found, possibly because of the low levels at which they were sampled.

DISCUSSION

Because of the small sample sizes involved, comparisons of the reproductive success of monogamous, primary and secondary females must be made cautiously. Nonetheless, certain trends appear to exist. Secondary females nested much later in the season than did primary females, with no temporal overlap within territories in two of three cases. Monogamous females present for the entire season showed a significant seasonal decrease in both clutch-size and number of young fledged. Because females paired to monogamous males often were double-brooded, while females paired to polygynous males were single-brooded (on my study area), the data suggest that females paired to monogamous males were most successful for the entire season (fledging 5.8 young per female, compared to

5.3 young for primary and 3.3 young for secondary females). It seems likely that several of the females I studied (e.g., YR, YG, GY; Fig. 2) were reproductively active off of my study area, making comparisons of seasonal reproductive success invalid. Primary females produced on average more young than did secondary females, but this may largely be a result of differences in nesting time and a general pattern of clutch-size reduction during the season. Neither primary nor secondary females differed substantially from monogamous females nesting at the same time.

The Orians-Verner-Willson model (Orians 1969, 1972; Verner and Willson 1966, 1969) and more recent amendments to the original model (Wittenberger 1976, 1979; Altman et al. 1977) deal primarily with species in which primary and secondary females share, in time, the resources available in a male's territory. Both food (Willson 1966) and nest-sites (Willson 1966, Holm 1973, Best 1977) have been indicated as critically distributed resources, such that males defending territories with abundant food and/or nest-sites are more likely to attract more than one female. This abundance theoretically compensates nesting primary and secondary females for the probable loss of male parental care, either in feeding young or defending young from predators.

The Orians-Verner-Willson hypothesis may also apply to species in which the nesting activities of primary and secondary females do not overlap, although there should perhaps be a change in emphasis away from food availability. Male parental care in this situation need not be reduced, and in habitats such as marshes where insects emerging throughout the season prevent depletion of food resources in territories, secondary females may not be subject to a reduction in food availability. In such situations variations in nest-site quality or availability may be the principal factor on which females base their choice of territories. Sedge Wren females do appear to choose their territories, at least in part, on the basis of the degree of protection from predators the vegetation offers. That polygynous males defended better nest-sites late in the season is suggested by the different rates of predation in the territories of monogamous and polygynous males. Predators (and possibly other wrens) destroyed none of the three late nests of polygynous males, while two of the eight nests of monogamous males were disrupted.

Intraspecific comparisons.—Two key differences exist between the population of Sedge Wrens studied by Crawford (1977) and the population reported on here. First, renesting by successful females did not occur in the population Crawford studied; second, Crawford found significant temporal overlap of the nesting activities of primary and secondary females paired to the same male. Various authors (Meanley 1952, Sherman 1952, Kroodsma and Verner 1978) have been impressed by the Sedge Wren's

opportunistic breeding strategy. Times of arrival vary substantially at a site from one year to the next. Birds present at a location in May can disappear by July, and the first arrivals in an area can be as late as mid-July (Meanley 1952, Sherman 1952, pers. obs.). During the 1976 season 12 males were present in the meadow, which I used for my study, early in the season. The following year only two males were present, neither of them banded, although laying had begun. Within a single breeding season males and females may abruptly appear or disappear from a meadow (Fig. 2). In short, Sedge Wrens are characterized by high mobility during the breeding season and low site tenacity between seasons. This opportunistic behavior may have selected for unique features in the communication system of Sedge Wrens (Kroodsma and Verner 1978) and therefore is presumably not of recent origin (say in response to agriculture). This opportunism adds another dimension of variability between populations, and may explain differences between populations of Sedge Wrens studied to date.

Interspecific comparisons.—Considerable variation occurs between populations of Marsh Wrens studied to date, probably due to gross differences in climate and habitat. The migratory habits of a population (resident or migrant) may be one factor influencing the social organization of a species (cf. Orians 1961, 1973; Verner 1965a) and therefore I will restrict my comparisons to the migratory eastern Washington Marsh Wrens studied by Verner (1965a) and Verner and Engelson (1970).

Male Sedge Wrens build about half as many nests as do Marsh Wrens (9 and 20, respectively), in territories that are 5–6 times as large (1800 and 300 m^2, respectively). Polygyny is present at approximately the same frequency in both species, with about one-third of the breeding males having more than one mate, but the overlapping of the nesting activities of primary and secondary females is more pronounced in Marsh Wrens. Several cases of trigamy have been reported for Marsh Wrens (Welter 1935; Verner 1964, 1965a), but none as yet has been recorded for Sedge Wrens. Both Sedge and Marsh wren females frequently renest after fledging young, and in neither species do males provide substantial amounts of parental care.

Most of these differences may be due to differences in food availability. Territories of Marsh Wrens vary substantially in average size from one population to another, variation suggested by Verner (1965a) to be a result of differences in food availability. An extension of his argument may be sufficient to explain the larger territories of Sedge Wrens. Orians (1980) discusses a general east to west trend of increasing secondary aquatic productivity, a trend possibly reflected interspecifically in territory size. Other differences, especially the greater amount of temporal overlap of

nesting primary and secondary female Marsh Wrens and the greater number of nests built by Marsh Wrens may also be explained by higher levels of food availability in the territories of Marsh Wrens, but this is largely conjecture.

Clearly what is needed to understand the quantitative differences between the two species is comparative information on time budgets, prey biomass per unit area and the nutritive values of utilized prey. Much of this information has already been obtained for Marsh Wrens (Kale 1965, Verner 1965b), and while the task of obtaining accurate time budget data on Sedge Wrens seems formidable, it would provide key information on the evolution of *Cistothorus* social systems.

SUMMARY

Twelve male Sedge Wrens (*Cistothorus platensis*) defended all-purpose territories averaging 1780 m^2, building an estimated average of nine nests each. Three of the males were polygynous. The mates of six monogamous males renested after successfully fledging young. Because of second nesting attempts, monogamous females averaged the highest fledgling success (5.8 young), followed by primary (5.3 young) and secondary (3.3 young) females. A seasonal decrease in clutch-size of monogamous females (from 7.0–5.7), combined with within season arrivals and departures of females confounds the analysis of reproductive success. Little difference was found between the success of different classes of females nesting at the same time. Polygynous males nonetheless achieved a higher mean reproductive success than did monogamous males, largely due to higher rates of predation on the late nests of monogamous males.

ACKNOWLEDGMENTS

I thank D. Bruggers, A. Burns, R. Crawford, L. H. Kermott, III, F. McKinney, H. B. Tordoff, J. Verner and M. F. Willson for comments on this paper and its earlier versions. Mark Heitlinger of the Nature Conservancy kindly gave permission to use the study site. W. D. Svedarsky contributed much logistical help, and D. Burns and P. Van Beckum helped with fieldwork. This work was funded by the Josselyn Van Tyne Student Research Award and the Wilkie Fund for Behavior and Evolution.

LITERATURE CITED

Altman, S. A., S. W. Wagner and S. Lenington. 1977. Two models for the evolution of polygyny. Behav. Ecol. Sociobiol. 2:397–410.

Bent, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers and their allies. U.S. Natl. Mus. Bull. 195.

Best, L. B. 1977. Territory quality and mating success in the Field Sparrow. Condor 79: 192–204.

Burns, J. T. 1977. Social organization of Short-billed Marsh Wrens. M.S. thesis, Univ. Minnesota, Minneapolis, Minnesota.

Crawford, R. D. 1977. Polygynous breeding of Short-billed Marsh Wrens. Auk 94:359–362.

Gibb, J. 1950. The breeding ecology of the Great and Blue titmice. Ibis 92:507–639.

Holm, C. 1973. Breeding success, territoriality and reproduction in the Red-winged Blackbird (*Agelaius phoeniceus*). Ecology 54:356–365.

KALE, H. W., II. 1965. Bioenergetics of the Long-billed Marsh Wren *Telmatodytes palustris griseus* (Brewster) in Georgia Salt Marshes. Publ. Nutt. Ornithol. Club 5.

KROODSMA, D. E. AND J. VERNER. 1978. Complex singing behaviors among *Cistothorus* wrens. Auk 95:703–716.

MARTIN, S. G. 1974. Adaptations for polygynous breeding in the Bobolink, *Dolichonyx orizivorus*. Am. Zool. 14:109–119.

MEANLEY, B. 1952. Notes on the ecology of the Short-billed Marsh Wren in the lower Arkansas rice fields. Wilson Bull. 64:22–25.

NICE, M. M. 1957. Nesting success of altricial birds. Auk 74:305–321.

ODUM, E. P. AND E. J. KUENZLER. 1955. Measurements of territory and home range in birds. Auk 72:128–137.

ORIANS, G. H. 1961. The ecology of blackbird (*Agelaius*) social systems. Ecol. Monogr. 31:285–312.

———. 1969. On the evolution of mating systems in birds and mammals. Am. Nat. 103: 589–603.

———. 1972. The adaptive significance of mating systems in the Icteridae. Proc. XV Int. Ornithol. Congr. 389–398.

———. 1973. The Red-winged Blackbird in tropical marshes. Condor 75:28–42.

———. 1980. Some adaptations of marsh-nesting blackbirds. Princeton Univ. Press, Princeton, New Jersey.

PICMAN, J. 1977a. Destruction of eggs by the Long-billed Marsh Wren (*Telmatodytes palustris palustris*). Can. J. Zool. 55:1914–1920.

———. 1977b. Intraspecific nest destruction in the Long-billed Marsh Wren (*Telmatodytes palustris palustris*). Can. J. Zool. 55:1997–2003.

ROYAMA, T. 1966. Factors governing feeding rates, food requirements and brood size of nestling Great Tits (*Parus major*). Ibis 108:313–347.

SALT, W. R. 1954. The structure of the cloacal protuberance of the Vesper Sparrow (*Poocetus gramineus*) and certain other passerine birds. Auk 71:64–73.

SHERMAN, A. R. 1952. Birds of an Iowa dooryard. Christopher Publishing House, Boston, Massachusetts.

STENGER, J. AND J. B. FALLS. 1959. The utilized territory of the Ovenbird. Wilson Bull. 71:125–140.

VERNER, J. 1964. Evolution of polygamy in the Long-billed Marsh Wren. Proc. XIII Int. Ornithol. Congr. 299–307.

———. 1965a. Breeding biology of the Long-billed Marsh Wren. Condor 67:6–30.

———. 1965b. Time budget of the male Long-billed Marsh Wren during the breeding season. Condor 67:125–139.

——— AND M. F. WILLSON. 1966. The influence of habitat on mating systems of North American passerine birds. Ecology 47:143–147.

——— AND ———. 1969. Mating systems, sexual dimorphism, and the role of male North American passerine birds in the nesting cycle. Ornithol. Monogr. 9.

——— AND G. H. ENGELSON. 1970. Territories, multiple nest building and polygamy in the Long-billed Marsh Wren. Auk 87:557–567.

WALKINSHAW, L. H. 1935. Studies of the Short-billed Marsh Wren (*Cistothorus platensis*) in Michigan. Auk 52:362–368.

WELTER, W. A. 1935. The natural history of the Long-billed Marsh Wren. Wilson Bull. 47:3–34.

WILLSON, M. F. 1966. Breeding ecology of the Yellow-headed Blackbird. Ecol. Monogr. 36:51–77.

WITTENBERGER, J. F. 1976. The ecological factors selecting for polygyny in birds. Am. Nat. 10:779–799.

———. 1979. The evolution of mating systems in birds and mammals. Pp. 271–349 *in* Handbook of behavioral neurobiology: social behavior and communication (P. Marler and J. Vandenburgh, eds.). Plenum, New York, New York.

DEPT. ECOLOGY AND BEHAVIORAL BIOLOGY, JAMES FORD BELL MUSEUM OF NATURAL HISTORY, UNIV. MINNESOTA, MINNEAPOLIS 55455. ACCEPTED 21 SEPT. 1981.

Wilson Bull., 94(3), 1982, pp. 350–354

GENERAL NOTES

Notes on migrants wintering at Monteverde, Costa Rica.—In the course of fieldwork at Monteverde, Costa Rica, from 15 December 1976–6 March 1977 we kept detailed notes on the abundances, habitat preferences, and behavior of migrant birds. Since much of our information has not been published elsewhere we present it here.

Monteverde is a small dairy farming settlement located on a high bench (1300–1650 m elev.) of the Pacific slope of the Cordillera de Tilarán (10°18′N, 84°49′W). Extensive tracts of both primary forest and man-altered habitats are present, and the area's unusually steep moisture gradient provides extraordinary life zone diversity. The lower edge of the bench (1300–1400 m) experiences a pronounced dry season (December–April) while the migrants are in residence, but higher elevations (1500+ m) are drenched almost continuously by wind-blown mist. Reflecting this moisture gradient, the climax vegetation changes as one climbs the bench from a semi-deciduous premontane moist forest whose canopy may be lower than 18 m, to an epiphyte-laden lower montane rain forest whose canopy generally exceeds 30 m (see Holdridge, Life Zone Ecology, Trop. Sci. Ctr., San Jose, Costa Rica, 1967). Details of the climate and physiography of Monteverde are provided by Buskirk and Buskirk (Am. Midl. Nat. 95:288–298, 1976) and Powell (Am. Birds 31:119–126, 1977). For more information on our procedures and for data on the foraging behavior of the seven commonest migrant warblers and vireos see Tramer and Kemp (pp. 285–296 *in* Migrant Birds in the Neotropics, Smithson. Inst., 1980).

Sharp-shinned Hawk (*Accipiter striatus*).—Single individuals were seen on five occasions between 25 December and 1 March, indicating a small wintering population. Sharp-shins were usually glimpsed as they darted silently across openings between patches of forest. Birds seen well were adult-plumaged.

Cooper's Hawk (*A. cooperii*).—One was seen briefly in premontane moist forest 20 February. Another large *Accipiter* was glimpsed in poor light on 16 December; it was probably either this species or a Bicolored Hawk (*A. bicolor*). Stiles (p. 431 *in* Migrant Birds in the Neotropics, Smithson. Inst., 1980) lists *A. cooperii* as rare in Costa Rica.

Broad-winged Hawk (*Buteo platypterus*).—This species was the most conspicuous raptor at Monteverde, encountered on 58 of our 74 days afield. It was common at the forest edge and in parkland habitats (pastures in which about half of the tall canopy trees had been left standing). It occurred at all elevations. All birds were solitary individuals in immature plumage. Broad-wings rarely soared, and kept mostly below the treetops. They were very vocal, using the same high-pitched sustained whistles heard on their North American breeding grounds. Individuals could be located at a given site for weeks at a time, suggesting the existence of small and faithfully kept home ranges.

Yellow-bellied Sapsucker (*Sphyrapicus varius*).—Lone sapsuckers were seen on four days between 28 December and 27 January. All were detected by their cat-like mewing notes; all were foraging at the edge of dense lower montane rain forest at elevations exceeding 1500 m.

Yellow-bellied Flycatcher (*Empidonax flavescens*).—We saw a singing bird of this species on 26 February at the edge of a pasture bordering premontane moist forest. Stiles (1980) lists this flycatcher as a common winter resident in the lowlands of Costa Rica. This apparently constitutes the first sighting of the species at Monteverde.

Barn Swallow (*Hirundo rustica*).—Barn Swallows are apparently rare on the bench itself, although we observed them on each of five visits to pastures in the foothills (500–1100 m). On 5 January we saw several birds feeding with Blue-and-white Swallows (*Notiochelidon cyanoleuca*) and Rough-winged Swallows (*Stelgidopteryx ruficollis*) during a hike just below the edge of the bench.

Wood Thrush (*Hylocichla mustelina*).—Powell (1977) lists this species as uncommon at Monteverde. However, we found it to be very common in premontane moist forest between 1300 and 1450 m. For the most part Wood Thrushes foraged quietly in leaf litter under heavy shade and were easily overlooked. The birds were most abundant on the sides of the steep-walled ravines that dissect the lower bench. There they occurred singly at intervals of 100–200 m, an even spacing suggestive of intraspecific territoriality, although we have no direct evidence for this. Occasionally, when flushed by a human intruder, a thrush would utter a rapid *pick-pick-pick* series identical to the alarm notes given by this species in North America.

Swainson's Thrush (*Catharus ustulatus*).—This bird is a scarce winter visitor to Monteverde; most individuals winter south of Costa Rica. We saw single birds on four occasions (16 December–13 February). Two sightings were of birds eating small fruits of two unidentified species of forest-edge trees. On both occasions Mountain Robins (*Turdus plebejus*), White-throated Robins (*T. albicollis*) and Mountain Elaenias (*Elaenia frantzii*) were eating fruit in the same trees but seemed indifferent to the thrushes' presence. In all four instances the thrushes were silent and inconspicuous, moving little and staying in dense foliage.

Yellow-throated Vireo (*Vireo flavifrons*).—We encountered this uncommon species on 18 of 74 days, always in the lower portion of the bench in the premontane moist forest or at its edge. The most notable thing about the species was its tendency to occur in pairs. We observed this arrangement in 16 of 23 sightings, and assume these to be male-female pairs because one bird was always brighter yellow and more clearly marked than the other. Yellow-throateds uttered occasional descending chatters or single scolding notes. They generally fed away from other species.

Solitary Vireo (*Vireo solitarius*).—A single bird was observed 30 December in a mixed foraging flock in premontane moist forest at 1375 m. It was very aggressive, chasing any small birds that approached within 1–2 m.

Philadelphia Vireo (*V. philadelphicus*).—This species was numerous at the forest edge below 1450 m, where we saw up to a dozen birds in a day. Philadelphias were less frequent in the forest interior and apparently absent above 1500 m. Like *V. flavifrons*, this species frequently occurred in pairs (well over 50% of our observations). This tendency runs counter to comments on these species by Slud (The Birds of Costa Rica, Bull. Am. Mus. Nat. Hist. 128:310, 312, 1964). Unlike *V. flavifrons*, Philadelphia Vireos often foraged with other species, especially Tennessee Warblers (*Vermivora peregrina*) and resident Brown-capped Vireos (*Vireo gilvus leucophrys*). They were usually silent, but we heard a bird in full song 28 February. Although all birds we observed were foraging for insects, we twice saw individuals regurgitate small fruit pits.

Black-and-white Warbler (*Mniotilta varia*).—This bird was fairly common below 1475 m elev. wherever there were large trees. This species foraged on trunks and large branches, similar to its behavior in North America. It often participated in mixed foraging flocks "led" by resident Golden-crowned Warblers (*Basileuterus culicivorus*), but consorted only rarely with conspecifics. No clear evidence of territoriality was noted, however.

Worm-eating Warbler (*Helmitheros vermivorus*).—Apparently this secretive species winters regularly at Monteverde in small numbers. We saw single birds on four occasions between 2 January and 21 February, but very limited mist netting (fewer than 10 net days altogether) by Richard T. Holmes in late January and by ourselves in February resulted in the capture of four others. All records were for elevations below 1500 m. Members of the species were silent and stayed in dense undergrowth. Tramer brought one to within 3 m by crawling into the midst of a dark thicket, sitting motionless and squeaking for 5 min. The results of limited mist netting suggest that the Worm-eating Warbler is more numerous at Monteverde than our few sight records indicate.

Golden-winged Warbler (*Vermivora chrysoptera*).—Individuals were scattered through the premontane moist forest. This species was also one of the few migrants occupying the interior of wetter forests above 1450 m, although it was scarce there. We saw this bird on 31 of 74 days. Although it frequently participated in mixed foraging flocks we never saw two golden-wings together. This species had extremely specialized foraging habits, probing in dead leaf clumps almost exclusively (also noted by Morton, Atlantic Nat. 27:164–168, 1972). On one occasion we saw a male take nectar (?) from the flowers of *Erythrina lanceolata* (Leguminosae).

Tennessee Warbler (*V. peregrina*).—This species was very common in parkland and woodland edges; it frequently fed in lone shrubs or isolated trees in open pastures. We rarely saw it in the forest interior. Tennessees stayed below 1500 m elev. and fed mostly within 12 m of the ground. They were the only migrant insectivorous species to form monospecific flocks (three or more birds), but individuals also defended feeding territories around blooming *Erythrina* trees, whose nectar apparently comprises an important energy source for this species. For details see Tramer and Kemp (Auk 96:186–187. 1979).

Black-throated Green Warbler (*Dendroica virens*).—Probably the most abundant migrant at Monteverde, this species occurred from 1300–ca. 1550 m, although it was most common at the lower elevations. It foraged from near the ground to high in the canopy, with a modal foraging height of 6 m. Isolated tall trees. parkland and woodland edges were its favorite habitats.

Townsend's Warbler (*D. townsendi*).—This close relative of *D. virens* was fairly common in edge situations between 1350 and 1500 m. It differed ecologically from *D. virens* in that it spent a much larger proportion of the time near the ground, and hawked after flying insects more frequently. W. Buskirk (Ph.D. diss., Univ. Calif., Davis, California, 1972) reported *D. townsendi* mostly in conifers at Monteverde, but we found it regularly in other vegetation as well. *D. townsendi* and *D. virens* were the only migrant warblers to initiate agonistic interactions with other species. A color slide taken by Kemp, now at the American Museum of Natural History, is the first tangible evidence of this species' occurrence in Costa Rica (E. Eisenmann, pers. comm.), although it is now known to winter south to western Panama (F. G. Stiles, pers. comm.).

Chestnut-sided Warbler (*D. pensylvanica*).—This uncommon species wintered in small numbers inside the premontane moist forest. We encountered it on only 12 days. Only single birds were seen, usually in loose association with small mixed foraging flocks led by *Basileuterus culicivoreus*.

Ovenbird (*Seiurus aurocapillus*).—Ovenbirds were common below 1475 m, where they foraged quietly in leaf litter on the forest floor. As in the vireos, we frequently saw two birds feeding close together.

Louisiana Waterthrush (*S. motacilla*).—Although Powell (unpubl.) lists waterthrushes as rare at Monteverde, we noted them on 11 occasions. It seemed that at least one bird resided in each deep ravine. We easily detected waterthrushes by walking ravine bottoms and listening for their loud *chip* alarm notes, given repeatedly as the birds flushed ahead of us. Waterthrushes were not encountered in any other habitat. Although the Northern Waterthrush (*S. noveboracensis*) has also been recorded at Monteverde, the four individuals we studied at close range had the pure white throat and superciliary stripe suggestive of *S. motacilla*.

Kentucky Warbler (*Oporornis formosus*).—This secretive bird of dense forest undergrowth was seen on only five occasions, but we often heard *chip* notes which we believe were this species, and limited mist netting in the premontane moist forest yielded an additional two to three birds daily. We conclude that a fairly large wintering population resides at Monteverde.

Wilson's Warbler (*Wilsonia pusilla*).—Wilson's Warblers were abundant, especially at

lower elevations on the bench. They stayed mostly within a few meters of the ground in dense cover, although a few birds were observed high in the canopy.

American Redstart (*Setophaga ruticilla*).—The only sight record for Monteverde is a lone bird we saw at the forest edge at 1450 m on 31 December.

Northern Oriole (*Icterus galbula*).—Orioles were common in parkland, citrus plantings, and edge habitats below 1400 m. They appeared singly or in small groups of both sexes. Orioles fed extensively on oranges, pecking 2-cm-wide holes in the peels and then gradually hollowing out entire fruits as they hung on the trees. Orioles also frequented *Erythrina* trees, where they are known to feed on nectar (F. G. Stiles, pers. comm.). All orioles seen were of the eastern (*I. g. galbula*) phenotype.

Summer Tanager (*Piranga rubra*).—This species was a fairly common denizen of parkland and woodland edge habitats, and occasionally occurred in the forest interior as well. We saw it on 33 days, and at elevations as high as 1525 m. The vast majority were males. Birds were often discovered by their *pi-tuck-tuck* call notes. They frequently hawked or hover-fed; we also suspected they were frugivorous since we often observed them in fruiting trees.

Western Tanager (*P. ludoviciana*).—The only record of this species at Monteverde was a dull specimen observed at the forest edge at 1350 m on 24 February. F. G. Stiles (pers. comm.) considers it common at lower elevations in Guanacaste Province, just northwest of Monteverde.

Rose-breasted Grosbeak (*Pheucticus ludovicianus*).—Single grosbeaks were seen on 2 January and 28 February in pasture trees at the lower edge of the bench (1350 m). The reasons for the scarcity of this species at Monteverde are unclear.

Indigo Bunting (*Passerina cyanea*).—This species was not listed for Monteverde by Powell (1977), but we found it to be fairly common in parklands and pastures below 1475 m. On several occasions flocks of more than two dozen were seen. The vast majority were in brown plumage.

Lincoln's Sparrow (*Melospiza lincolnii*).—Tramer (Wilson Bull. 91:469–470, 1979) obtained the first sight records of this species for Costa Rica. The three sightings were in grassy or weedy situations, two in fields and one on a roadside. Although the observations spanned 30 days and occurred 1 km apart, all could conceivably have involved a single bird.

Other species.—Four other migrant species were encountered during our stay. These also nest in Costa Rica, so it is impossible to know whether the birds we saw were migrants. These species are (1) Turkey Vulture (*Cathartes aura*), an abundant migrant through Central America (N. Smith, pp. 51–65 *in* Migrant Birds in the Neotropics, Smithson. Inst., 1980) but also resident at Monteverde; (2) Swallow-tailed Kite (*Elanoides forficatus*), a species seen on three occasions late in our stay; (3) Red-tailed Hawk (*Buteo jamaicensis*), seen three times in late February; and (4) Rough-winged Swallow (*Stelgidopteryx ruficollis*). The swallow was common at Monteverde; both breeding and migrant forms are likely there (see Stiles, Auk 98:282–293, 1981) but we did not attempt to distinguish them.

The rapid pace of deforestation in the tropics has caused concern for the future of long-range migrant birds (see Terborgh, p. 23 *in* Migrant Birds in the Neotropics, Smithson. Inst., 1980). At Monteverde the extensive forest plays a vital role in the ecology of many migrant species. Of the 29 migrants discussed above, all save three appear to be dependent on at least some forest cover. For most of those species patches of second growth woodland with edge may be sufficient. However, eight species (Cooper's and Sharp-shinned hawks, Wood Thrush, Worm-eating, Chestnut-sided and Kentucky warblers, Ovenbird, and Louisiana Waterthrush) were birds of the forest interior whose continued presence at Monteverde may well depend on the preservation of sizeable tracts of mature forest. Most of the protected mature forest at Monteverde is wet forest not favored by migrants. Therefore, the future of the eight species listed above may well depend on the preservation of the premontane moist forest, currently unprotected.

We are grateful for the assistance of many people at Monteverde, and to F. Gary Stiles for a critical review of an earlier version of this paper. Tramer was supported by grant DEB 76-10787 from the National Science Foundation and a sabbatical leave from the University of Toledo.—Elliot J. Tramer and Thomas R. Kemp, *Dept. Biology, Univ. Toledo, Toledo, Ohio 43606.* *Accepted 10 Dec. 1981.*

Wilson Bull., 94(3), 1982, pp. 354–355

Decline of the Roadrunner in Missouri.—A gradual northeastward range expansion of the Roadrunner (*Geococcyx californianus*) has been documented over the past 50 years. In the late 19th century Goss (History of the Birds of Kansas, Geo. W. Crane and Co., Topeka, Kansas, 1891) described the Roadrunner's range as being "northern Mexico, north to southern Colorado and California, east into Texas and southwest Kansas." Expansion of this range into eastern Kansas and Oklahoma was first reported in the 1930's (Colvin, Auk 52:88, 1935). Sutton (*in* Bent, U.S. Natl. Mus. Bull. 176, 1940) cited the Roadrunner's range as extending east to south-central Kansas and central Oklahoma. Subsequent extension in Arkansas was reported by Baerg (Condor 52:165, 1950) and James (Arkansas Acad. Sci. Proc. 14:8–13, 1960). First documentation of Roadrunners in Missouri was by Brown (Condor 65:242–243, 1963) who reported 12 sightings in the southwestern part of the state dating back to 1956. Probasco (5th Midwest Prairie Conference Proc., Iowa St. Univ., Ames, Iowa, 1976) provided further documentation of the bird in Missouri. This northeast expansion coincided with range extensions northward in California (Kimsey, Condor 55:215, 1953) and Utah (Hayward et al., Great Basin Naturalist Memoirs, Birds of Utah, No. 1, Brigham Young Univ. Press, Provo, Utah, 1976) and eastward into Louisiana (Lowery, Louisiana Birds, Louisiana State Univ. Press, Baton Rouge, Louisiana, 1955).

To further document the range expansion of the Roadrunner in Missouri, a survey by Jim Rathert within the Missouri Department of Conservation provided information on many sightings of Roadrunners in southern Missouri. All sightings were made or substantiated by Conservation Agents familiar with the avifauna of the area. Based on these results and extensive personal communication with bird watchers, Breeding Bird Census participants and Audubon Christmas Count personnel, we determined that the Roadrunner's range continued to expand both north and east in Missouri until 1976. By this time Roadrunners had been sighted throughout 36 counties in southern Missouri, extending north to the Missouri River (Fig. 1) but centered in the glade areas of the southwestern part of the state.

Beginning with the severe winter of 1976–77, the Missouri population of Roadrunners began a decline which continued through 1978–79, probably due to three successive severe winters. The 1978 distribution was much reduced from previous years (Fig. 1). The Audubon Christmas Bird Count data for Oklahoma also showed a decline from 26 Roadrunners sighted in 1976 to 17 in 1977 and one in 1978, despite an increase in the number of observers (Am. Birds, Vols. 31–33, 1977–1979).

Decline of the Missouri Roadrunner population may have been caused by starvation indirectly brought about by severe winter weather. Although Roadrunners are highly opportunistic feeders and eat a variety of small vertebrates, they rely on invertebrates, chiefly insects, during the nonbreeding season (Bryant, Univ. Calif. Publ. Zool. 17:21–50, 1916; Sutton, Bull. Oklahoma Ornithol. Soc. 5:30, 1972).

Climatic data for the region were studied to investigate the possible role of severe winter weather in preventing Missouri Roadrunners from obtaining food. During the period of active range expansion in Missouri, winter weather was characterized by snow cover that was

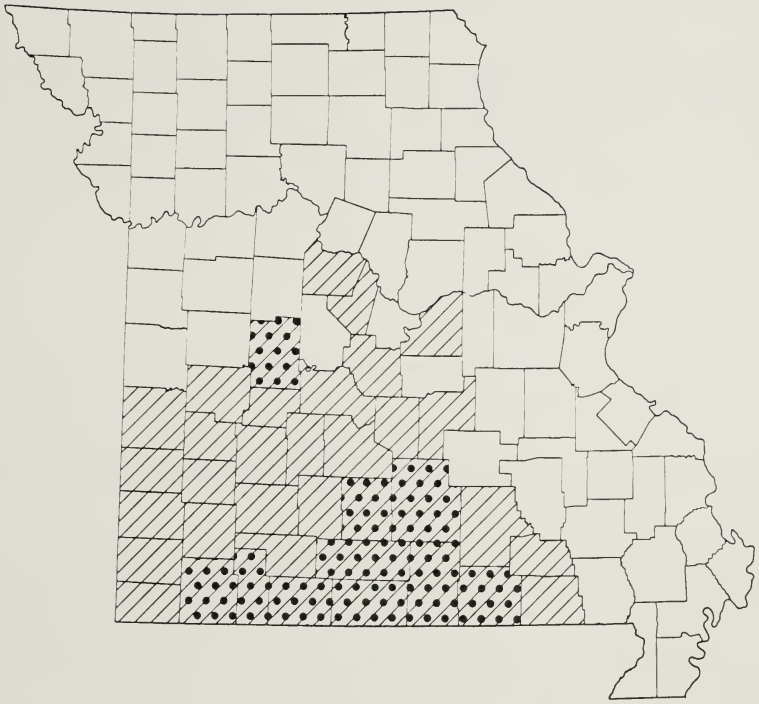


FIG. 1. Distribution of the Roadrunner in Missouri, showing the counties occupied in 1976 (diagonal lines) and 1978 (dotted areas).

generally light and short in duration. The mean daily snow cover was 1.4 cm in January (the severest month) and the mean number of snow days was 7.9. Beginning with the winter of 1976–77 and continuing in 1977–78 and 1978–79, snow cover was heavy and persistent. The mean daily snow cover was 18.0 cm, 11.2 cm and 11.6 cm in January of the 3 years, respectively, and the number of snow days were 29, 22 and 31, respectively. It may be that these periods of prolonged snow cover prevented the birds from obtaining prey, especially insects and reptiles, resulting in starvation. On 23 January 1979, a Roadrunner in weakened condition was found in Pulaski County, Missouri; it subsequently died. Postmortem examination showed that the gastrointestinal tract was empty and the bird's weight was 202 g, less than half that of healthy Roadrunners in December in Oklahoma (Geluso, Bull. Oklahoma Ornithol. Soc. 2:5–6, 1969). Snow cover at the time of capture was heavy and had been continuous for 25 days.

The observations reported herein suggest that the Missouri Roadrunner population declined between 1976 and 1979 during a period of unusually severe winters.

Acknowledgments.—This study was funded in part by the USDA Forest Service, Cooperative Research Agreement 13-666. We thank Keith E. Evans and George E. Probasco of the Forest Service for their valuable assistance.—DOUGLAS J. NORRIS AND WILLIAM H. ELDER, *Missouri Cooperative Wildlife Research Unit, School of Forestry, Fisheries and Wildlife, Univ. Missouri, 112 Stephens Hall, Columbia, Missouri 65211.* *Accepted 5 Jan. 1982.*

Wilson Bull., 94(3), 1982, pp. 356–358

The occurrence and behavior of non-breeding Horned Puffins at Black Guillemot colonies in northern Alaska.—The Black Guillemot (*Cepphus grylle*) and Horned Puffin (*Fratercula corniculata*) are cavity nesting alcids that typically breed in talus. In Alaska both species breed in rock cavities as far north as Cape Lisburne (D. Roseneau, pers. comm.). No talus or rock cliffs are present north of Cape Lisburne but the Black Guillemot has extended its breeding range to the northern Chukchi and Beaufort seas by breeding in man-made debris (Divoky et al., Condor 76:339–343, 1974). Censuses north of Cape Lisburne from 1972–1981 show the following number of Black Guillemot breeding pairs at the major colonies (Fig. 1): 5—Seahorse Island, 5—Point Barrow, 20—Deadman Island, 100—Cooper Island, and 5—Igalik Island. Bailey (Birds of Arctic Alaska, Pop. Ser. 8, Colorado Museum of Nat. Hist., 1948) considered the Horned Puffin a rare vagrant north of Cape Lisburne. During extensive pelagic and inshore censusing of the northern Chukchi and Beaufort seas Horned Puffins were seen in fewer than 1% of all observation periods (Divoky, pers. obs.). This note documents the regular occurrence of Horned Puffins at Black Guillemot colonies in northern Alaska and describes previously unrecorded behaviors of non-breeding puffins at guillemot nest-sites. These behaviors include the displacement of guillemot eggs, and the feeding, brooding and killing of guillemot chicks.

Two- to 3-h censuses of Black Guillemot colonies have produced sightings of Horned Puffins. At Seahorse Island two were seen on 6 and 30 July 1972, one on 5 August 1976 and two on 25 July 1981. The puffins were associated with a sand dune that had burrows with alcid footprints leading into them. The burrows were too deep to be completely examined for the presence of eggs or young. Black Guillemot nests at Seahorse Island were primarily in a natural driftwood pile. At Deadman Island a single Horned Puffin was seen on 15 and 20 August and 6 September 1976, and 4 September 1977. Two were present on 14 August 1979 and 18 August 1980, and four on 3 July and 13 August 1981. All sightings of puffins at Deadman are of birds circling the barge containing guillemot nests.

The most systematic observations of Horned Puffins have been at Cooper Island where Black Guillemots breed in boxes and other man-made debris. Periods of observation were 16 June–16 September 1976, 21 June–20 August 1977, 1 July–12 September 1978, 26 June–5 September 1979, 9 June–7 September 1980, and 4 June–7 September 1981. Horned Puffins were seen mostly from mid- to late summer until early September when observations ceased. Dates of first sightings were 4 August 1976, 2 August 1977, 7 July 1978, 16 July 1979, 24 June 1980, and 16 June 1981. Because all behavioral information was gathered at Cooper Island it it important to note that the number of puffins encountered was small. Sightings were usually of a single bird, although two were seen frequently in 1979 and 1980, and four were seen on one instance in 1979. All of our observations of puffins at nest-sites may have been of the same bird. A puffin banded at a guillemot nest-site in 1978 returned to Cooper Island the next 3 years.

Few puffin-guillemot interactions were observed away from nest-sites. Guillemots occasionally chased a puffin in the air. Single puffins frequently sat next to guillemot flocks, both on land and water. While Drent (Ardea 53:99–160, 1965) observed Pigeon Guillemots (*C. columba*) giving a communal alarm call at the approach of a Tufted Puffin (*Lunda cirrhata*), We observed no similar behavior.

Horned Puffins entered Black Guillemot nest-sites on Cooper Island. With the exception of observations in 1980, Horned Puffins entered only nest-sites with chicks. In 1980 a single puffin entered a nest shortly after eggs were laid.

We have primarily circumstantial evidence of puffin activities in nest-sites. In 1980 eggs in six guillemot nests were pushed out of their depressions 1–7 days after laying. All nests

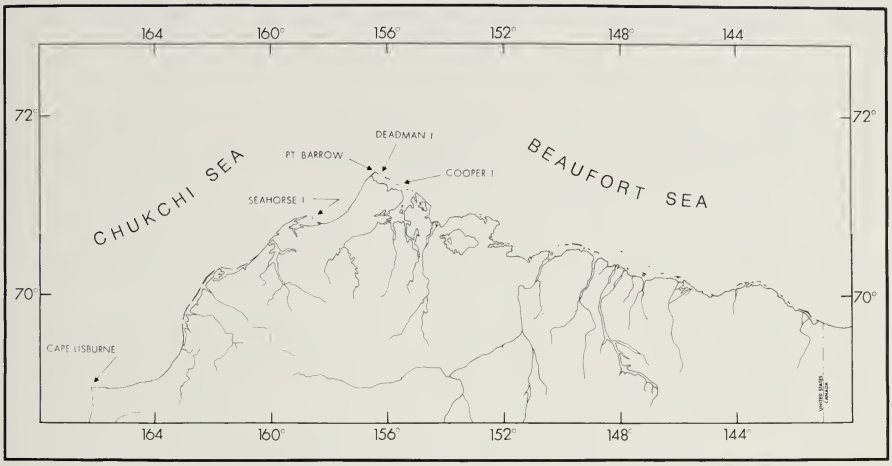


FIG. 1. The location of Black Guillemot colonies in northern Alaska mentioned in the text.

affected were next to a pond frequented by a puffin and a puffin was seen entering a nest where eggs were later found to be displaced. No egg displacement occurred in other areas of the colony.

In 1978, 1979, and 1980, Horned Puffins were observed brooding guillemot chicks. One instance was recorded in 1978 when a puffin was found brooding two chicks. In 1979 two chicks in one nest-site were brooded by a puffin between 14 and 27 August for 16 of 46 h of observation. On two occasions a puffin brooded the chicks continuously for at least 4.5 h while the parents fed the chicks. Feeding occurred at the nest-site entrance without the parents entering, a not unusual method of feeding. In 1980 there were two instances of a puffin brooding two chicks at one nest-site.

On six occasions in 1979 a puffin circled the colony with a fish in its bill. In four instances the puffin entered a nest-site with a fish and brooded the chicks. It could not be determined if the fish were consumed by the chicks or the puffin. Fish were brought only to the site where chicks were regularly brooded by a puffin and presumably all brooding and "feeding" involved the same puffin.

There is some evidence that Horned Puffins may kill or injure adult and nestling guillemots in or near nest-sites. A total of 11 deaths (nine chicks and two adults) were recorded from 1976–1980: three chicks in one nest (1976); two chicks and one adult in the same site (1977); one adult in a nest-site (1978); two chicks on one nest-site and one in another (1979); one chick (1980). Puffins were observed at nest-sites where deaths subsequently occurred. Dead chicks had either crushed skulls, or head and neck wounds. No puffin-related mortality occurred at the sites where a puffin regularly brooded in 1979 and 1980. However, one of the two chicks brooded in 1979 had holes bitten or torn in the webs of its feet and both chicks brooded in 1980 had wounds in the nape region.

Nest-building by puffins occurred in 1979 and 1980 at sites where a puffin regularly brooded. In 1979 six feathers were placed in the site. In 1980 the guillemot eggs were displaced in the same site and the gravel floor excavated to create a larger cavity. The site regularly visited in 1980 had over 40 feathers placed in it in a 2-day period in late August.

This is the first reported instance of an alcid displacing the eggs or killing the young of a

species with which it competes for nest-sites. It is also the first record of interspecific chick brooding and feeding in alcids. Intraspecific brooding and feeding of chicks has been observed in murres (*Uria* sp.) (Perry, Lundy: Isle of Puffins, Lindsay Drummond, London, England, 1946).

(*Addendum 1982.*—On 8 July 1982, a pair of Horned Puffins arrived at Cooper Island and courted at Black Guillemot nest-sites where later eggs of the latter species were found to have been pushed out of nest depressions. No observations of puffin courtship activities have previously been made at the islands discussed herein.)

Acknowledgments.—This study was supported by the Outer Continental Shelf Environmental Assessment Program (OCSEAP) of the Bureau of Land Management and the National Oceanographic and Atmospheric Administration. Logistical support was provided by the Naval Arctic Research Laboratory in Barrow. J. C. Bartonek, R. J. Boekelheide, A. E. Good, and T. L. McElroy assisted in field observations. D. H. S. Wehle and S. G. Sealy commented on an earlier draft of this note.—George J. Divoky, *College of the Atlantic, Bar Harbor, Maine 04609.* *Accepted 20 Nov. 1981.*

Wilson Bull., 94(3), 1982, pp. 358–361

Body temperature and growth of Bonin Petrel chicks.—Body temperature and timing of endothermy in several altricial and semi-altricial species have been related to the length of the nestling period (Dawson and Evans, Physiol. Zool. 30:315–327, 1957), the growth rate constant k (Ricklefs and Hainsworth, Condor 70:121–127, 1968; Dunn, Condor 77:286–291, 1975), feeding history of the chick (Wheelwright and Boersma, Physiol. Zool. 52:231–239, 1979), and the mass of the nestling (Marsh, Physiol. Zool. 52:340–353, 1979). Data for small procellariiforms are meager but they suggest that the semi-altricial chicks are able to maintain adult body temperatures within a few days of hatching (Farner and Serventy, Condor 61:426–433, 1959; Wheelwright and Boersma 1979). Growth among procellariiform chicks is characterized by slow development, a long and flexible fledging period, large deposits of lipid reserves, and achievement of pre-fledging weights well above the adult's body weight, followed by a pre-fledging weight loss. These growth characteristics are considered to be adaptations to meager, distant, or fluctuating food resources (Lack, Ecological Adaptations for Breeding in Birds, Methuen, London, England, 1968). In addition, procellariiform birds have prolonged incubation periods and slow embryonic growth rates which may be related to slow growth of the chick after hatching (Ackerman et al., Physiol. Zool. 53:210–221, 1980; Whittow, Am. Zool. 20:427–437, 1980). A recent visit to Midway Islands in the northwestern Hawaiian Islands presented us with an opportunity to measure the growth and fledging period of Bonin Petrel (*Pterodroma hypoleuca*) chicks, the thermal environment of their nest-burrows, and development of body temperature regulation.

Methods.—Chicks were weighed twice daily at 07:00 and 17:00 with a torsion balance (±0.1 g) up to 2 weeks of age and then with Pesola spring scales (±1 g) until fledging. At 2 weeks of age chicks were banded for subsequent identification and measurement. Growth data from 1980 and 1981 have been pooled and a logistic growth equation fitted to the data (Ricklefs, Ecology 48:978–983, 1967). Data are presented as means ± 1 SD.

The Bonin Petrel nests in a deep burrow (Grant et al., Auk 99:236–242, 1982); a pre-constructed shaft provided access to the nest-chamber. The temperatures of both incubating adults and chicks were obtained by inserting a sheathed thermocouple into the proventriculus. Temperatures were measured with a Kane-May Ltd. Dependatherm. Ambient temperatures of burrows were recorded continuously over several days on a linear recorder, with the thermocouple placed about 10 cm from the incubating petrel.

Table 1
Growth Parameters of Two Species of Tropical Petrels

Parameter	Bonin Petrel	Dark-rumped Petrel[a]
Asymptote, a	250	400–500
Adult weight, W (g)	182	385
R = a/W	1.37	1.04–1.30
Fledging weight, FW (g)	206	340–360
FW/W (%)	113	88–94
k	0.091	0.061–0.076
ka/4 (g × day^{-1})	5.69	6.10–9.50
kR/4 × 100 (% × day^{-1})	3.12	1.59–2.47
t_{10-90} (4·4/k, days)	48.35	72.13–57.89
Fledging period (days)	82	109–112

[a] Data for two chicks, computed separately, from Harris (1970).

Results.—After an external pipping-(shell fracture)-to-hatch interval of 5–6 days, during which "peeping" may be heard for about 3 days, the chick emerges after having cracked the shell near the blunt pole of the egg (Pettit et al., Physiol. Zool. 55:162–170, 1982). After drying, the hatchling is light grey dorsally, becoming lighter ventrally to whitish on the abdomen, resembling chicks of many petrel species. The eyes open within 48 h and the tarsi gradually darken from pale grey with flesh-colored webbing on the feet, to a darker grey overall, after

Fig. 1. Mean daily weights (g) of Bonin Petrels on Midway Atoll in 1980 and 1981. Open circle is value for a single chick.

TABLE 2
MEAN WEIGHT GAIN (G) OVER 24 H AND MEAN BODY TEMPERATURE (°C) OF BONIN PETREL CHICKS

	24 h weight gain			Body temperature		
Age (days)	$\bar{x}$	±SD	N	$\bar{x}$	±SD	N
1	7.7	3.7	8	37.2	0.8	11
2	9.5	3.3	9	38.3	0.5	7
3	11.1	5.6	10	38.2	0.4	5
4	8.4	6.6	8	38.2	0.2	4
5	12.3	10.1	9	37.7	0.3	2
6	18.9	9.3	7	37.8	0.2	3
7	10.4	6.7	6	38.1	0.2	3
8	9.9	4.9	5	38.3	0.4	4
9	19.8	15.5	8	—	—	—
10	17.5	14.8	9	38.0	0.8	3
11	19.9	14.0	6	38.2	0.4	3
12	17.4	16.7	6	38.3	0.6	3
13	13.0	9.7	7	38.5	—	1
14	19.4	12.9	6	38.5	0.4	3
15–60	—	—	—	38.2	0.4	26

3–4 weeks. This developmental sequence is similar to that of other *Pterodroma* spp. (Warham, Emu 67:1–22, 1967; Warham et al., Auk 94:1–17, 1977). The white egg-tooth disappeared from the characteristically thick bill at a mean age of 9.9 ± 2.0 days (N = 14). Adults brood chicks for only 1–2 days post-hatching, but may return to spend an additional day in the nest-chamber during the first week of feeding. Chicks are initially fed regurgitated proventricular oil and later small pieces of squid and fish. Chicks may regurgitate oil upon handling but do so infrequently.

Mean daily weights of Bonin Petrel chicks (N = 12–19) are presented in Fig. 1. The logistic growth equation fitted to the data is $W_t = 250/1 + e^{-0.091(t-19.3)}$, $r = 0.985$ where W_t = weight (g) of chick at age t (days); e is base of natural logarithms, 2.72; and r is the correlation coefficient. Table 1 presents growth parameters based upon the logistic equation. Fledging occurred at a mean age of 82.2 ± 2.8 days (N = 5) and a mean weight of 206.0 ± 23.9 g (N = 5). The mean maximal recorded weight was 282.5 ± 35.5 g (N = 14), and occurred at a mean age of 56.8 ± 7.1 days (N = 14). The absolute maximum weight was 341 g (187% of adult weight) in one chick 51 days old.

In 36 of 140 (26%) measurements of body weight during the first 2 weeks post-hatching there was a net loss of weight over 24 h ranging from 1.1–36.3 g, the result of little or no feeding. Chicks are generally fed during the night and only 4 of 120 measurements of weights showed a net increase during a 10-h daytime period. Table 2 presents the mean weight gains over a 24-h period during the first 2 weeks post-hatching. On the second day after hatching a chick was fed 14.5 g or 52% of its body weight. The largest relative amount of nocturnal feeding was recorded in a 10-day-old chick which was fed 53.5 g or 61% its body weight. Maximum overnight weight gain was 79 g in a 24-day-old chick.

Mean body temperature of 11 incubating adults measured during the day was 37.0 ± 0.1°C. The mean ambient burrow air temperature (N = 3) recorded between 31 January and

3 March 1980 was 17.1 ± 0.3°C. During mid-March, burrow air temperatures increased to 20–22°C (mean 20.8 ± 0.7°C, N = 11).

On the first day post-hatching, 9 of 11 chicks were brooded and had mean body temperatures of 37.2 ± 0.8°C as compared with a body temperature of 35.8°C in an unbrooded, 1-day-old chick. By age 2–3 days post-hatching (Table 2) chicks attained mean adult body temperature (38.2 ± 0.6°C; Udvardy, Auk 80:181–194, 1963). With no feeding for 2 days, the body temperature of a single chick, aged 5 days, was 24.0°C at an ambient burrow temperature of 20.5°C. After feeding by the parent of about 30 g of regurgitated food, the body temperature rose to 38.2°C the next day.

Discussion.—Attainment of adult body temperatures by petrel chicks at a relatively early age (2–3 days) may free parents from brooding, allowing foraging at sea soon after hatching. The early metabolic and thermoregulatory independence of Bonin Petrel chicks is partially due to the relatively stable micro-environment of the nest-chamber, which is typical of other burrow-nesting procellariiforms (Farner and Serventy 1959; Howell and Bartholomew, Condor 63:185–197, 1961; Wheelwright and Boersma 1979). In addition, it is not unusual for brooded or freshly hatched procellariiform chicks to have body temperatures higher than the brooding adult (Farner and Serventy 1959; Howell and Bartholomew 1961; Pettit and Whittow, unpubl.).

Diurnal body temperatures of incubating Bonin Petrels averaged 37.0°C in this study, which is significantly lower ($P < 0.05$, Student's t-test) than the mean incubation temperature of 38.5°C reported by Howell and Bartholomew (1961). Udvardy (Auk 8:191–194, 1963) reported a mean body (rectal) temperature of 38.2°C in non-incubating Bonin Petrels resting on the ground at night on Laysan Island. Our value (37.0°C) is at the lower extreme of those reported for 31 species of Procellariiformes (Warham, Condor 73:214–219, 1971). Our petrel body temperatures were recorded by simply pulling the bird out through the preconstructed shaft and rapidly inserting the thermocouple. Howell and Bartholomew (1961) dug out their birds to take their body temperatures. Perhaps this digging was stressful enough to elevate the body temperature of the petrels measured by these authors.

The growth parameters of two Dark-rumped Petrel (*Pterodroma phaeopygia*) chicks from the Galapagos Islands (Harris, Condor 72:76–84, 1970) are presented for comparison with the Bonin Petrel (Table 1). The logistic growth rate constant, k, is 0.091 in the Bonin Petrel and 0.061 and 0.076 for the two Dark-rumped Petrel chicks, indicating a slower rate of growth for the larger dark-rumped chicks. Other growth parameters such as t_{10-90}, i.e., the amount of time (days) required to grow from 10–90% of the asymptotic weight, also indicate slower growth in Dark-rumped Petrels. Growth data for other tropical members of this genus have not been published.

Acknowledgments.—Our stay on Midway Atoll was supported by NSF Grant PCM76-12351A01 administered by G. C. Whittow. We are indebted to the U.S. Fish and Wildlife Service for granting permits to conduct this study. We thank Mr. Russell Shea, Dept. Biology, University of Pennsylvania, for collecting additional data following our departure from Midway.—Ted N. Pettit, Gilbert S. Grant, and G. Causey Whittow, *Dept. Physiology, John A. Burns School of Medicine, Univ. Hawaii, Honolulu, Hawaii 96822.* (Present address: GSG *N.C. State Museum of Natural History, P.O. Box 27647, Raleigh, North Carolina 27611.*) *Accepted 5 Dec. 1981.*

Wilson Bull., 94(3), 1982, pp. 361–362

Prolonged incubation behavior in Common Loons.—Prolonged incubation has been documented for many bird species (Skutch, Parent Birds and Their Young, Univ. Texas Press, Austin, Texas, 1976) but has not previously been reported for the family Gaviidae.

During the summers of 1977 and 1979 two instances of prolonged incubation by Common Loons (*Gavia immer*) for 74 and 68 days, respectively, were observed in New Hampshire. Normal incubation periods reported for the species in New Hampshire range between 25–33 days and average 28 days (Sutcliffe, Aspects of the Nesting Ecology of Common Loons in New Hampshire, M.S. thesis, Univ. New Hampshire, Durham, New Hampshire, 1980). In both cases reported herein the loons were monitored at least twice weekly and chances of egg loss followed by renesting were unlikely. Both nests were ultimately abandoned. The 74-day clutch (two eggs) was found in the nest, whereas eggs from the 68-day clutch were found floating adjacent to the nesting island. All eggs were addled and their contents were about one quarter the volume of a normal loon egg. Reasons for non-viability were undetermined.

These examples serve to verify Skutch's (1976) observations that some bird species may remain faithful to unhatched, malodorous eggs for periods up to twice the normal incubation length, thereby providing a wide margin of safety for eggs taking longer to hatch. At northern latitudes, where short ice-free seasons may reduce the possibilities for renesting and fledging of chicks before freeze-up, this behavior may be beneficial to loon populations. However, in more southern areas like New Hampshire, where ice-free seasons are longer, prolonged incubation of non-viable eggs may prevent successful renesting that might occur otherwise.

I am grateful to Loon Preservation Committee staff members Ralph Kirshner, Connie Manville, Kim Young and volunteer Joe Comolli for aid in field observations. Don Miller and Lloyd Kiff provided valuable suggestions and help with the manuscript.—SCOTT SUTCLIFFE, *The Nature Conservancy, Box 72, Cold Spring Harbor, New York 11724.* *Accepted 10 Dec. 1981.*

Wilson Bull., 94(3), 1982, pp. 362–363

Barn Swallow fledgling successfully elicits feeding at a non-parental nest.—In Barn Swallows (*Hirundo rustica*), as in many species, the begging behavior of fledglings is ignored by the parents just prior to independent feeding. Fledglings then beg indiscriminately from any available conspecific. They are usually disregarded and begin to feed independently. Herein, I report on an instance of a fledgling successfully obtaining food from an adult which was not its parent. On 20 July 1980, while watching a nest in a Barn Swallow colony of 80 pairs under the decks of the Rutgers Marine Field Station, I saw a fledgling from another nest land in the nest I was watching and beg with the nestlings; the nest contained four 14-day-old nestlings. The female at this nest had previously been banded and color marked on her breast. Her mate was unmarked. The young Barn Swallow, identified as a fledgling by its breast color and yellow gape, landed on the edge of the nest. Both adults were there and called vociferously at the intruding bird. The intruding young remained at the nest despite this and the adults left after 60 sec. For 10 min the intruder crouched in the nest cup behind the nestlings. It then began to present its gape (which was noticeably larger than those of the nestlings) to the feeding adults. During the next 30 min the female made seven feeding trips to the nest and the male made ten. On two trips the intruder was fed by the male.

The adults apparently recognized the fledgling as an intruder. Immediately after feeding it for the first time the male pecked at it. On three other occasions the male paused after feeding his own young and tried to evict the intruder by pecking at it. All of these attempts usually lasted less than 1 min. The second time the fledgling was fed, the male stayed fewer than 10 sec at the nest.

This observation is consistent with what is known about individual recognition in Barn

Swallows. Although Burtt (Anim. Behav. 25:231–239, 1977) has shown that Barn Swallows do not start to recognize their young until the time of fledging, Grzybowski (Condor 81:236–246, 1979) demonstrated that parents can discriminate between their own young and experimentally presented young of a different developmental stage. The intruder's success in acquiring food on two feeding visits from adults in 30 min was probably a function of the severe time constraints on parents with broods of this age and size. The parents averaged 20–30 feeding visits per hour which left little time to remove the intruder from the nest and increased the probability of making a mistake since many of the visits were brief. Similar feeding errors in Bank Swallows (*Riparia riparia*) have been reported (Hoogland and Sherman, Ecol. Monogr. 46:33–58, 1976; Beecher et al., Anim. Behav. 29:86–94, 1981). But in this species, as in Barn Swallows, the parents are usually able to chase off or evict alien fledglings.

I would like to thank C. Beer, S. Lenington, K. Sullivan, C. Brown and R. Wolinski for reading and making comments on this note.—Gregory Ball, *Institute of Animal Behavior, Rutgers Univ., 101 Warren Street, Newark, New Jersey, 07102.* *Accepted 15 Nov. 1981.*

Wilson Bull., 94(3), 1982, pp. 363–365

Cowbird control and its effect on Kirtland's Warbler reproductive success.— Kirtland's Warbler (*Dendroica kirtlandii*) is the subject of international interest and was officially listed in the U.S. as an endangered species in 1967 because of its precarious status. Reasons for the decline of the Kirtland's Warbler population are complex and not fully understood. Parasitism of warbler nests by Brown-headed Cowbirds (*Molothrus ater*) has been suggested as one cause. Kirtland's Warbler is particularly vulnerable to nest parasitism (Mayfield, The Kirtland's Warbler. Cranbrook Inst. Sci., Bloomfield Hills, Michigan, 1960).

Since 1972 the U.S. Fish and Wildlife Service has conducted an intensive program of cowbird removal in the Kirtland's Warbler nesting areas in the northern lower peninsula of Michigan. Shake and Mattsson (Jack-Pine Warbler 53:48–53, 1975) reported on cowbird control efforts from 1972–1974. The present report summarizes the Fish and Wildlife Service's cowbird control program and its effect on warbler nesting and fledging success from 1975–1981.

Cowbird decoy traps were erected on nesting areas located in Crawford, Kalkaska, Ogemaw, Oscoda, Iosco, and Roscommon counties in Michigan. The number of traps in operation varied from 28–40 during 1975–1981. Traps were placed at approximately square mile (1.6 km^2) intervals within nesting areas. A more detailed description of decoy traps and trapping methods is given by Shake and Mattsson (1975). The nesting data for 1972–1981 were collected by Nicholas Cuthbert and Lawrence Walkinshaw under contract with the U.S. Fish and Wildlife Service.

During 1975–1981, 24,158 cowbirds were removed from the Kirtland's Warbler nesting areas, an average of 3451 birds per year. When combined with data from 1972–1974 the total number of cowbirds removed by trapping is 33,536 (Table 1).

Concomitant with the cowbird control program there was a substantial decrease in cowbird parasitism on Kirtland's Warbler nests. Walkinshaw (Am. Birds 26:3–9, 1972) reported that from 1931–1971, 59% (54 of 91) of Kirtland's Warbler nests examined were parasitized. In 1972, the parasitism rate dropped to 6% (2 of 31) of the nests examined (Fig. 1). Cowbird parasitism of Kirtland's Warbler nests has ranged from 0–9%, and averaged 3.4% over the 10 years of the cowbird control program.

Table 1

Brown-headed Cowbirds Removed from Kirtland's Warbler Nesting Areas in Michigan, 1972–1981

Year	Males	Females	Juveniles	Totals
1972–1974[a]	5659	3421	298	9378
1975	2026	1463	161	3650
1976	2223	1964	112	4299
1977	1845	1405	34	3284
1978	1754	1639	18	3411
1979	1959	1722	10	3691
1980	1538	1429	0	2967
1981	1770	1085	1	2856
Totals	18,774	14,128	634	33,536

[a] Shake and Mattsson (1975).

In conjunction with the reduction in the parasitism rate, there was a substantial increase in the number of young warblers fledged per nest examined. Walkinshaw (1972) reported that warbler nests averaged fewer than one young fledged per nest during the period 1931–1971. In 1972, the number of young fledged per nest (mean clutch-size = 4.22) averaged 2.84

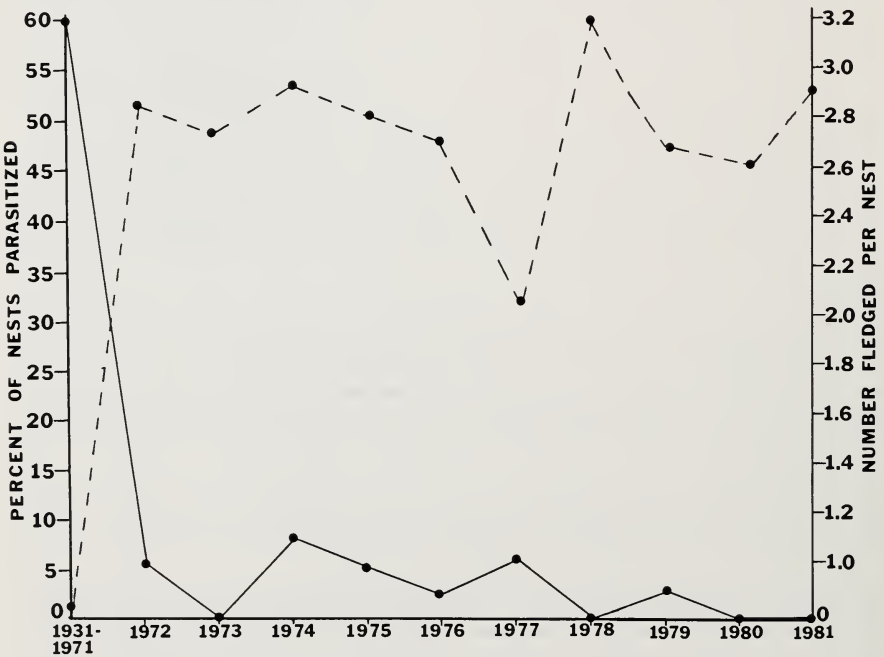


Fig. 1. Kirtland's Warbler fledging success in relation to cowbird parasitism on nesting areas in Michigan.

(Shake and Mattsson 1975) and during the subsequent 9 years of the cowbird control program the average number of young fledged per nest per year has varied from 2.1–3.2 with an average of 2.76 young fledged over the 10 years of cowbird removal (Fig. 1).

The principal objective of the U.S. Fish and Wildlife Service's cowbird control program is to reduce cowbird parasitism of warbler nests and consequently increase the total Kirtland's Warbler population. In spite of the cowbird control program, the Kirtland's Warbler population has not increased substantially. In 1971 the census of Kirtland's Warblers revealed the presence of 201 singing males (Mayfield, Auk 82:263–268, 1972). The annual survey of singing male Kirtland's Warblers during the 10 years of cowbird control has varied from 167–243 birds and averaged 207 (Ryel, Jack-Pine Warbler 59:93–95, 1981).

The adverse effects of cowbird parasitism have long been recognized; however, other factors influencing Kirtland's Warbler population levels are not well defined. The Kirtland's Warbler has very specific nesting habitat requirements, needing young jack pine (*Pinus banksiana*) stands of fire origin. Studies are being conducted to determine the critical vegetation requirements of their breeding habitat (Buech, Jack-Pine Warbler 58:59–72, 1980).

The lack of increase in Kirtland's Warbler numbers also emphasizes the need for information on the warbler after fledging, during migration, and on the wintering grounds in the Bahama Islands. Researchers have speculated that wintering conditions may be more severely limiting than the breeding habitat (Mayfield, Jack-Pine Warbler 53:39–47, 1975; Ryel, Jack-Pine Warbler 59:76–91, 1981).

Considering the data indicating greatly reduced nest parasitism and increased nesting success, it is evident the cowbird control program on the Kirtland's Warbler nesting areas has been successful. The cowbird control program appears to have been essential to the survival of this endangered species. However, additional research is needed to identify and evaluate factors which continue to limit Kirtland's Warbler population levels.

We gratefully acknowledge the cooperation and financial support of the Michigan Department of Natural Resources, Michigan Audubon Society, and the U.S. Forest Service.—Sean T. Kelly, *U.S. Fish and Wildlife Service, 200 North High Street, Columbus, Ohio 43215* and Michael E. DeCapita, *U.S. Fish and Wildlife Service, East Lansing, Michigan.* *Accepted 15 Nov. 1981.*

Wilson Bull., 94(3), 1982, pp. 365–366

Unusual nest sanitation by a Broad-winged Hawk.—The following observations were made from a tree blind placed 7.5 m horizontally from and 1 m above a Broad-winged Hawk (*Buteo platypterus*) nest 3.9 m up in a trembling aspen (*Populus tremuloides*) in Lincoln County, Wisconsin. Three times on 21 June 1980, one of us observed the same tending adult fly less than 1 m down from a perch in the nest tree to the nest and nibble at the recently excreted feces from a brood of two (4 and 5 days old). The feces had not cleared the nest and one of two nest-supporting tree trunks. We believe the hawk consumed the feces because much of the excreta had disappeared and at no time did it shake its head to rid the beak of the material. We obtained two photographs of this hawk with stains of feces on its beak and observed this behavior by this adult on six other occasions. The behavior sequence was usually as follows: the perched adult would watch as a nestling showed intention movements (rump elevation and backing toward nest rim) preparatory to defecation; when the ejected feces did not clear the nest and/or support trunk, the adult would instantly jump to the nest and nibble at the debris clinging to the nest or tree. The adult always consumed feces which were deposited on the nest or its supports during the 84 h and 39 min of observation from

21–26 and 28–29 June. By 30 June the young (about 14 days old) were able to excrete clear of the nest and its supports and we never again observed this adult consume feces.

Most young raptors are able to eject feces clear of the nest. Ellis (Wildl. Monogr. 70, 1979) stated that adult female Golden Eagles (*Aquila chrysaetos*) nibble their young to remove feces and other debris. Snyder (Living Bird 13:73–97, 1974) reported that parent Swallow Tailed Kites (*Elanoides forficatus*) at one nest continually covered the youngs' feces which had not cleared the nest with vegetation. We found no other accounts of raptors removing feces from a nest or its supports.

We would like to thank C. Rosenfield and D. Ledger for their assistance, and D. Ellis and H. Mueller for their review of this note.—Robert N. Rosenfield, *College of Natural Resources, Univ. Wisconsin–Stevens Point, Stevens Point, Wisconsin 54481*, Adam J. Rosenfield, *610 Wallace Avenue, Duluth, Minnesota 55812*, and Michael W. Gratson, *College of Natural Resources, Univ. Wisconsin–Stevens Point, Stevens Point, Wisconsin 54481.* *Accepted 15 Nov. 1981.*

Wilson Bull., 94(3), 1982, p. 366

First record of a Bald Eagle nest in West Virginia.—In May 1981, George Hall notified the Raptor Information Center of a Bald Eagle (*Haliaeetus leucocephalus*) nest located along the south branch of the Potomac River near the town of Moorefield, West Virginia. He reported that a pair of Bald Eagles spent the winter in the area and began nest building in early February. We contacted the caretaker of the property and arranged to examine the nest.

The nest was at a height of 12 m in a red oak (*Quercus rubra*) and appeared much smaller than nests of this species observed by the authors in the Chesapeake Bay region. The small size (1.5 m in diameter by 0.5 m deep) suggested that this was the first year the eagles nested at this site. The nest tree is on a steep bank, making it possible to look down into the nest. On 16 June 1981 the nest contained two eaglets which, because of their size and plumage, appeared to be approximately 7–8 weeks of age.

Although there are numerous sight records of Bald Eagles in West Virginia, we have found no previous nesting records. Bald Eagles have been sighted during two previous summers approximately 25 km south of this nest-site near Franklin, Pendleton Co. (Phillips, Redstart 47(1):46, 1980).

We thank M. R. Fuller and W. S. Clark for comments, G. A. Hall for his review and comments and for the initial information which led to the verification of this nest, and to Barry Levaas for reporting the sighting and for leading us to the nest-site.—Maurice N. LeFranc, Jr., Thomas A. Pierson, and Michael G. May, *Raptor Information Center, National Wildlife Federation, 1412 16th St., N. W., Washington, D.C. 20036.* *Accepted 14 Dec. 1981.*

Wilson Bull., 94(3), 1982, pp. 366–368

Osprey spreads wings after fishing.—Other than cormorants (*Phalacrocorax* spp.) and anhingas (*Anhinga* spp.), few birds that wet their plumage during foraging show maintenance behavior such as wing spreading and shaking (Rijke, J. Exper. Biol. 48:185–189, 1968). Whereas several authors report that Ospreys (*Pandion haliaetus*) shake their plumage after

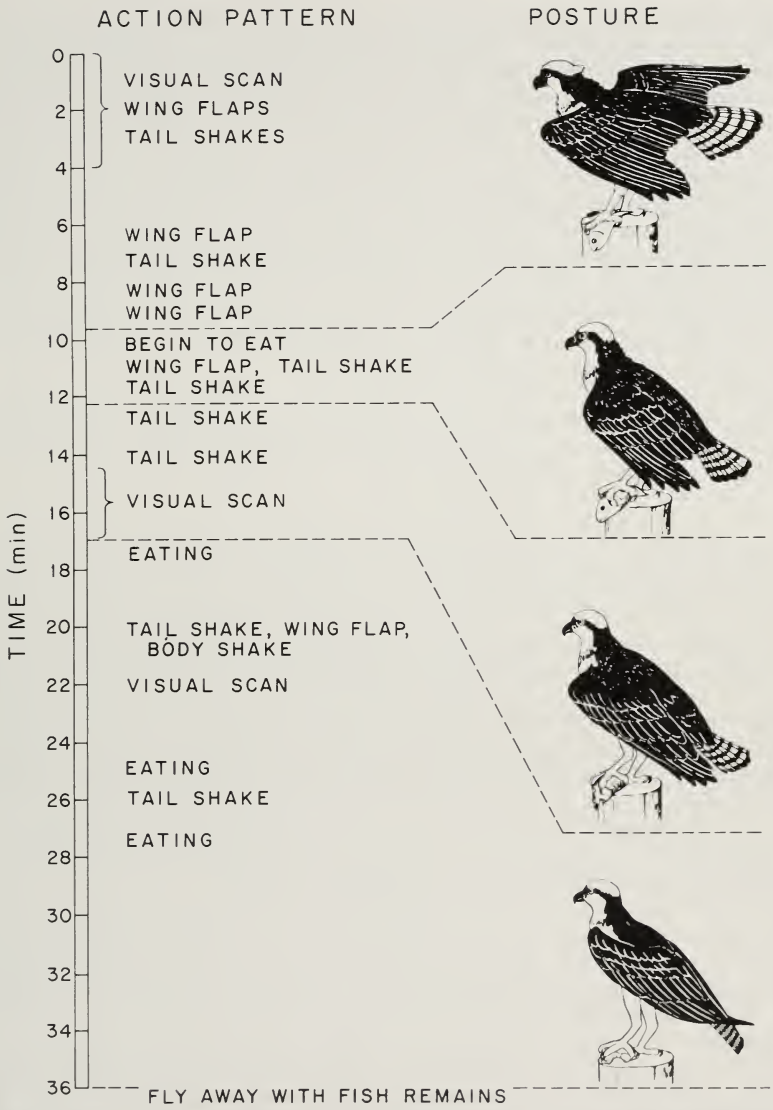


FIG. 1. Time line of the Osprey's spread-wing posture and associated behavior, observations begin at the top with time zero.

they dive for prey (Bent, U.S. Natl. Mus. Bull. 167, Pt. 1, 1937:367; Sprunt, North American Birds of Prey, Harper and Bros., New York, New York, 1955:129) none report wing spreading. In the spring of 1980, I observed an Osprey do so.

Observations began at 16:15 EST in clear weather at the southern tip of the Everglades National Park in Dade County, Florida, when an Osprey carried a fish, probably a mullet

(Mugilidae), to an old pier piling 90 m SE of my position. Using 7× binoculars, I noted that the bird was wet about the head, neck, and breast, although I could not judge the wetness of the wings due to their position. A minute later, the Osprey began a sequence of postures and actions similar to those of wet anhingas and cormorants (Clark, Auk 86:136–139, 1969). A detailed, running account of the wing positions and associated behavior is illustrated in Fig. 1.

It may be that the Osprey's posture was not due to wet plumage but to some other cause. One possibility is that the bird was hunched over its prey to protect it from piracy by other predatory birds. Bent (1937) described an Osprey which, upon the arrival of its mate, spread its wings and tail and crouched over its catch until the offender flew off. However, save for an immature Laughing Gull (*Larus atricilla*), there were no other birds in the immediate vicinity of the piling nor any other predatory birds in the general bay area that I could see. Also, the spread-wing posture was held for more than 7 min before the arrival of the gull; therefore, a protective motivation does not seem likely.

Acknowledgments.—I am grateful to J. P. Hailman, K. L. Bildstein, and R. Bancroft for their criticisms which greatly improved the manuscript. I acknowledge the skill of Cheryle Hughes who did the illustration.—A. M. Elowson-Haley, *Dept. Zoology, Univ. Wisconsin, Madison, Wisconsin 53706.* *Accepted 15 Dec. 1981.*

Wilson Bull., 94(3), 1982, pp. 368–369

Rough-winged Swallows scavenging adult midges.—Wolinski (Wilson Bull. 92:121–122, 1980) reported Rough-winged Swallows (*Stelgidopteryx ruficollis*) landing and feeding on fly larvae on dead fish on a Lake Huron beach. As this swallow seldom lands on the ground (see also Lunk, Publ. Nuttall Ornithol. Club, No. 4, 1962) this behavior probably represented opportunistic foraging in response to a temporary, high-density food source.

In the morning of 31 May 1980, for 10 min from ca. 5 m, I observed four Rough-winged Swallows standing on wet sand 0.5 m from the water's edge of Lake Manitoba (ca. 5 km west of Delta, Manitoba). The birds fed continuously on dead midges (Diptera: Chironomidae) that had washed ashore. I did not observe aggressive interactions by any individuals in the flock, despite their feeding within a few centimeters of each other.

Other swallow species are abundant summer residents and visitants in this area, but this is only the second time I have recorded *Stelgidopteryx* here in 7 years of work on passerine ecology. A juvenile was mist-netted on 9 August 1978. I have seen no other species of swallows taking dead midges or other insects in the manner described above, although I often have seen Barn Swallows (*Hirundo rustica*) picking up nesting material on this lakeshore.

Annually in this area, massive emergences of midges occur frequently from May through August (Busby and Sealy, Can. J. Zool. 57:1670–1681, 1979; Biermann, M.Sc. thesis, Univ. Manitoba, Winnipeg, Manitoba, 1980). In 1980, the first emergences transpired on 26 May and swarming adult midges were abundant until 6 June. Dead individuals were first noticed on the beach and elsewhere by 28 May.

Diptera comprise about 33% of the diet of *Stelgidopteryx* (Beal, USDA Bull. 619, 1918; Bent, U.S. Natl. Mus. Bull. 179, 1942). However, as Wolinski (1980) pointed out, these insects are generally taken aerially. That the prey were dead and hence the swallows were scavenging (see McNicholl, Can. Field-Nat. 91:416, 1977) reveals a plasticity in this swallow's feeding that has not been reported previously. While the swallows fed on the dead midges, live midges swarmed only a few meters away. As I did not see the flock land, I do not know

whether it was the windrowed midges to which the swallows first responded. The dead midges appeared fresh and their nutritional content was likely still similar to that of living midges. The swallows exploiting this clumped, stationary food source probably used less energy than they would in aerial pursuit. Such hypothesized conservation of energy might have been important if the swallows had flown a long distance the previous day or night.

Acknowledgments.—My work on passerine ecology has been funded by grants from the Natural Sciences and Engineering Research Council of Canada (A9556) and the University of Manitoba Research Board. The continued support of J. M. Shay, Director, and the staff and students of the University of Manitoba Field Station (Delta Marsh) is greatly appreciated. H. R. Carter and R. A. Wishart offered helpful suggestions on the mansucript, as did also the referees, J. P. Hailman and E. E. Klaas. The present contribution is publication No. 77 of the University of Manitoba Field Station (Delta Marsh).—Spencer G. Sealy, *Dept. Zoology, Univ. Manitoba, Winnipeg, Manitoba R3T 2N2 Canada.* *Accepted 1 Oct. 1981.*

Wilson Bull., 94(3), 1982, pp. 369–372

Diet of Glaucous Gulls in western Alaska.—The Glaucous Gull (*Larus hyperboreus*) is an arctic circumpolar species that has received attention because its diet includes economically important species of fish and birds (Olson, Fed. Pittman-Robertson Rept., Proj. 3-R-6:34–62, 1951; Uspenski, Can. Dept. North. Aff. and Nat. Resour., 1958; Belopolskii, Israel Prog. Sci. Transl., Jerusalem, Israel, 1961). With one exception (Olson 1951), however, large-sample diet studies of this gull have been conducted only in the northern Atlantic and European areas.

This report describes a comparative field study of Glaucous Gulls in two different habitats near the Bering Sea, in western Alaska. The coastal study area was at Kokechik Bay (60°40′N, 166°W), on the western tip of the Yukon-Kuskokwim Delta of Alaska, within Clarence Rhode National Wildlife Range. I used this area from 20 June–17 August 1972 and 10 May–17 August 1973. Gulls at the coast nested both in colonies and as isolated pairs.

The inland study area, 40 km SE of the coastal area, was 11 km from the nearest point on the Bering Sea coast. I used this area from 26 April–9 September 1974 and 11 June–2 July 1979. Inland Glaucous Gulls bred only in isolated pairs. Both study areas are less than 3 m above mean sea level and are subject to floods.

I determined the diet of Glaucous Gulls from stomach contents, and from regurgitated pellets and food remains collected at nests (food remains are items too large to be organized into pellets by the digestive tract). Weathered pellets and food remains from previous years were not collected. The stomachs for 1972 were collected by D. Eisenhauer (Eisenhauer and Kirkpatrick, Wildl. Monogr. 57:1–62, 1977) at Kokechik Bay.

I summarized the data as percentage of stomachs, pellets, and food remains containing each food category (i.e., as percent frequency occurrence). Lumping together different sources of food data appears to be justified. Pellets and food remains were collected at the same time in the same manner. In 1972, the only year from which sufficient numbers of both stomachs and other food data are available for comparison, the stomachs, pellets, and food remains ranked the food categories similarly, except for a bias in favor of mammals in the pellets plus food remains, and a bias in favor of terrestrial invertebrates in the stomachs. With few exceptions, the more limited data from other years support this result. Statistical analysis of the data comprised χ^2 comparisons, interpreted conservatively ($P \leq 0.01$) by consideration of patterns of differences rather than results of individual tests.

Table 1

Percent Frequency Occurrence of Foods in Glaucous Gull Stomachs, Regurgitated Pellets, and Separate Items of Food Remains at Nests

Year (location)	1972 (coast)	1973 (coast)		1974 (inland)		1979 (inland)	
Time relative to gull hatch peak	After	Before	After	Before	After	Before	After
Sample sizes							
Stomachs	26	8	40	0	15	0	0
Pellets	17	65	4	40	117	29	33
Food remains	39	17	9	20	64	29	18
Food categories							
Mammals	6.1	57.8	1.9	25.0	1.5	10.3	2.0
Adult birds	24.4[a]	5.6	0.0	16.7	30.6	32.8	25.5
Eggs, downy young		21.1	22.6	36.7	39.8	36.2	60.8
Fish	67.1	51.1	66.0	38.3	47.4	19.0	15.7
Marine invertebrates	22.0	6.7	30.2	15.0	9.7	12.1	7.8
Terrestrial invertebrates	4.9	2.2	15.1	0.0	1.0	0.0	0.0
Marine vegetation	6.1	3.3	0.0	0.0	0.0	0.0	0.0
Terrestrial vegetation	1.2	2.2	9.4	0.0	2.0	0.0	2.0

[a] Combined avian foods.

The coastal gulls' diets did not differ between years (Tables 1, 2; only data collected after the gull hatch were compared). The single exception in the terrestrial invertebrates category is the result of the sampling bias mentioned earlier; when the test is made with only stomachs, the difference disappears ($\chi^2 = 0.35$, df = 1, $P > 0.01$).

Only one food category was consistently different between years in the inland gulls' diet. The reduced emphasis on fish in 1979 is coincident with the absence of a potential terrestrial competitor, the red fox (*Vulpes vulpes*), which, together with the resident Arctic fox (*Alopex lagopus*) population, devastated the waterfowl nests in 1974. An unusual series of severe storms in 1979 also may have made eggs more available to gulls by causing nest abandonment, and may have increased the availability of crippled adult birds. Although foxes potentially could help gulls by disturbing nests, there is evidence (Strang, J. Wildl. Manage. 44:220–222, 1980) that Glaucous Gulls may not take advantage of such opportunities. The importance of competitive pressure from foxes is uncertain; however, there are no consistent differences between 1974 and 1979 in the gulls' use of avian foods. Fish might simply have been more abundant in 1974.

The only consistent change in diet within a single breeding season on both study areas was in the frequency of mammal consumption (Tables 1, 2). The mammals, nearly all of which were tundra voles (*Microtus oeconomus*), were consumed heavily prior to the median gull egg hatching date, when the rodents were exposed and crowded on hilltops by spring floods.

I pooled data between years to compare diets of coastal and inland Glaucous Gulls (Tables 1, 2). Birds (mostly waterfowl) were more important foods for inland gulls than for coastal gulls, and fish were more important for coastal gulls. Marine invertebrates were more important for inland gulls before the gull eggs hatched, and for coastal gulls after the hatch. None of the remaining food categories showed consistent differences between study areas.

Table 2

Chi-square Values from Comparisons of Glaucous Gull Diets (Percent Frequency Occurrence of Each Food Category Considered Separately) between Locations, between Years, and between Times

Comparison (sample sizes)	Mammals	Adult birds[a]	Eggs and downy young	Fish	Marine invert.	Terrestrial invert.	Marine veg.	Terrestrial vegetation
Between locations (coast vs inland)								
Before gull hatch (90 and 118)	77.4**	80.5**	16.7**	23.5**	8.9**	2.7	4.0	2.7
After gull hatch (135 and 247)	4.6	22.3**	65.2**	51.6**	33.0**	20.0**	9.5**	3.4
Between years								
1972 vs 1973 (82 and 53)	1.6	0.1		0.0	2.1	11.8**	3.4	6.4
1974 vs 1979								
Before gull hatch (60 and 58)	6.6**	10.7**	0.0	9.2**	0.4	0.0	0.0	0.0
After gull hatch (196 and 51)	0.1	0.6	9.5**	20.6**	0.2	0.5	0.0	0.0
Between times (before vs after gull hatch)								
1973 (90 and 53)	67.7**	3.2	0.1	4.7	45.8**	39.4**	1.8	12.3**
1974 (60 and 196)	57.6**	27.3**	0.8	6.9**	4.3	0.6	0.0	1.2
1979 (58 and 51)	19.6**	1.6	14.8**	0.5	1.5	0.0	0.0	1.2

[a] Data on adult birds, eggs and downy young combined for the 1972 vs 1973 comparison.
** $P < 0.01$, df = 1 for each test; sample sizes obtained from Table 1.

Most of the fish consumed by Glaucous Gulls were cod (*Eleginus gracilis*), both at the coast, where at least 61% of the fish taken were of this species, and inland, where the proportion was at least 78%.

The availability of eggs and young birds was greater on the inland study area. Eisenhauer (M.Sc. thesis, Purdue Univ., Lafayette, Indiana, 1976) estimated that 5315 waterfowl nests were present at Kokechik Bay in 1973. The availability per gull averaged 8.2 nests, considerably lower than my estimate of 28.2 waterfowl nests per inland gull in 1974. The latter estimate is based on waterfowl nest densities I measured on a 411.4-ha lowland tundra subset of the inland study area, with an extrapolation to the remaining lowland parts of that study area. Time constraints limited my search to pond edges in 1979, and several potentially nest-swamping storms had occurred before my search began, so the estimate of nest availability is lower than in 1974, at 20.2 nests per gull, but still is higher than the coastal availability in 1973.

Densities of marine invertebrates and dislodged *Fucus* (the only marine plant consumed by the gulls) generally are much higher at the coast. *Eleginus* moves to the deeper ocean waters in summer (Andriyashev, Israel Prog. Sci. Transl., Jerusalem, Israel, 1954), and so should have been more available at the coast than on the inland rivers.

I do not believe that inland gulls flew to the coast to feed, for three reasons. (1) I noted the directions of 39 departures or arrivals of gulls leaving or entering three nesting territories on 19 different days between 19 May and 26 July 1974. Only 7.7% of those arrivals or departures were in the quadrant closest to the sea (southwest), 48.8% were in the quadrant closest to the Kashunuk River (southeast), and the remainder were divided almost equally between the other two quadrants (northwest and southeast). (2) Furthermore, inland gulls did not exhibit the coastal gulls' tide-related activity pattern. Gulls in large numbers flew over the river channel in Kokechik Bay at low tide, surface plunging for fish, and then walked ahead of the rising water's edge to pick up invertebrates and *Fucus* from the intertidal zone mud. At high tide, Glaucous Gulls were nearly absent from the bay. Such a pattern was not evident among the isolated pairs nesting inland at the Kashunuk River in 1974, where the numbers of inland gulls passing observation points on the Kashunuk River within 2 h of low tide ($\bar{x}$ = 7.71 gulls per session, N = 14 two-h observation sessions) were not different from numbers of gulls passing at other times ($\bar{x}$ = 9.60 gulls per session, N = 20; Mann-Whitney *U*-test, $z = -0.94$, $P > 0.05$). (3) Finally, the species of invertebrates eaten by inland gulls (isopods and small clams) were not the same as those eaten by colonial gulls nesting near the mouth of the Kashunuk River. On one visit to the colonies in early August 1974, I noticed that the accumulated pellets and food remains were nearly all of a distinctive clam species different from those consumed by inland gulls; remains of other invertebrates, fish, etc., were relatively scarce. Isopods, clams and *Eleginus* all occur within the inland study area, which is close enough to the coast for the tidal flux to reverse the Kashunuk's direction of flow routinely.

The bulk of this paper is part of a Ph.D. dissertation, supervised by C. M. Kirkpatrick and submitted to Purdue University in May 1976. The research was sponsored by the National Wildlife Federation, the American Petroleum Institute, the Frank M. Chapman Memorial Fund of the American Museum of Natural History, and the Dickinson College Research and Development Fund. I received help in the field from Calvin J. Lensink, Jerry L. Hout, Christian P. Dau, Ann H. Strang, and Gary L. Strang.—CARL STRANG, *Biology Dept., Dickinson Co., Carlisle, Pennsylvania 17013.* (Current address: *Forest Preserve District of DuPage County, Willowbrook Wildlife Haven, 525 S. Park Blvd., Glen Ellyn, Illinois 60137.*) *Accepted 20 Nov. 1981.*

Wilson Bull., 94(3), 1982, pp. 372–381

Vocal behavior of the Northern Oriole.—The vocal behavior of several species of Icteridae has been described, e.g., Red-winged Blackbird (*Agelaius phoeniceus*) (Orians and Christman, Univ. Calif. Publ. Zool. 84, 1968; Smith et al., Condor 82:259–266, 1980), Brown-headed Cowbird (*Molothrus ater*) (West et al., J. Comp. and Physiol. Psychol. 93:124–133, 1979), Common Grackle (*Quiscalus quiscula*) (Ficken, Auk 80:52–72, 1963; Wiley, Anim. Behav. 24:570–584, 1976), Western Meadowlark (*Sturnella neglecta*) (Fish et al., Am. Zool. 2:409, 1962; Falls and Krebs, Can. J. Zool. 53:1165–1178, 1975), and Eastern Meadowlark (*S. magna*) (Lanyon, Bull. Am. Mus. Nat. Hist. 134:1–26, 1966), but little information on vocalizations exists for *Icterus* spp. The purpose of this note is to describe the vocalizations of male Northern (Baltimore) Orioles (*Icterus galbula galbula*), and particularly the song variation found in one locality in Michigan.

Methods.—This study was conducted in an area of approximately 140 ha in Kensington Metropark, located in Oakland County in southeastern Michigan, from 9 May–25 June 1980.

Table 1

Length and Frequency Characteristics of Songs of Male Orioles

Male	No. songs measured	$\bar{x}$ song length (sec)	$\bar{x}$ low frequency (kHz)	$\bar{x}$ high frequency (kHz)	$\bar{x}$ frequency range (kHz)
1	80	1.27 ± 0.280	1.8 ± 0.12	3.7 ± 0.21	1.8 ± 0.21
2	18	1.19 ± 0.203	1.9 ± 0.03	3.7 ± 0.10	1.8 ± 0.12
4	20	1.25 ± 0.335	1.9 ± 0.11	3.8 ± 0.30	2.0 ± 0.35
5	20	0.98 ± 0.312	1.5 ± 0.16	3.6 ± 0.14	2.1 ± 0.22
13	139	1.50 ± 0.458	1.9 ± 0.17	4.3 ± 0.46	2.4 ± 0.47
15	17	1.16 ± 0.078	1.8 ± 0.05	3.9 ± 0.08	2.0 ± 0.10
16	16	1.19 ± 0.373	1.8 ± 0.08	3.8 ± 0.61	2.0 ± 0.66
18	20	2.02 ± 0.271	1.6 ± 0.11	3.6 ± 0.19	2.0 ± 0.25
19	11	2.47 ± 0.502	1.9 ± 0.14	4.2 ± 0.51	2.4 ± 0.60
21	20	0.93 ± 0.319	1.7 ± 0.24	3.7 ± 0.07	2.0 ± 0.28
22	18	1.03 ± 0.310	2.0 ± 0.04	4.0 ± 0.31	2.0 ± 0.30
25	14	1.77 ± 0.589	1.5 ± 0.08	3.9 ± 0.33	2.3 ± 0.48
27	14	1.43 ± 0.428	1.9 ± 0.09	3.4 ± 0.13	1.5 ± 0.14
30	20	1.50 ± 0.295	2.0 ± 0.08	3.9 ± 0.41	1.9 ± 0.43
Total	427	—	—	—	—

Observations and recordings were made from 05:00–09:00 EST. Oriole vocalizations were recorded at 9.5 cm/sec with a Uher 4000 Report IC tape recorder equipped with a Uher 517 microphone and a 61-cm aluminum parabolic reflector. Wide band sonagrams for song analysis were prepared using a Kay Elemetrics Sona-Graph, model 6061B, connected to a Tandberg series 15 tape recorder.

To familiarize myself with the behavior of orioles, two males (no. 1 and no. 13) were observed and recorded regularly throughout the breeding season as defined above. Male 1 was observed for 25 h over 19 days and male 13 was observed for 90 h over 20 days. Songs of other males were also recorded. Orioles were not banded but most males were readily recognizable as individuals by their characteristic songs and commonly used song-posts.

Males arrived on the study area during the second week of May and established territories that were usually contiguous with those of other orioles. Females arrived on the territories 2–14 days after the males. Little courtship could be observed because of the density of the foliage. Females built nests after searching for nesting material, generally within the confines of the territory. Eggs were laid from late May through early June. Males made frequent trips to the nest during the incubation and nestling stages of the breeding cycle; both males and females fed the nestlings. The young fledged within 2 weeks of hatching. For the purposes of data analysis, the oriole breeding season was divided into four periods: (1) before the females arrived on the males' territories, (2) after female arrival, but before incubation, (3) incubation, and (4) the nestling period.

Song length, song frequencies, and song figure characteristics were all measured directly from sonagrams. Song figures were transferred to tracing paper and were tested against one another for similarities and differences by attempting superimposition. A song figure was arbitrarily defined as a continuous trace on a sonagram, or a series of traces separated by no more than 20 msec. Two figures were considered to be identical when they were superimposable on tracing paper. Slight deviations in duration and/or frequency were tolerated to

Table 2

Song Figure Characteristics and Song Pattern Repertoire Sizes of 14 Male Orioles

Male	No. songs measured	$\bar{x}$ No. figures/song	$\bar{x}$ No. figure types/song	No. figure types in figure repertoire	No. different song patterns sung
1	80	8.5 ± 0.91	3.3 ± 0.51	5	8[b]
2[a]	18	7.6 ± 1.22	5.7 ± 0.69	6	3
4	20	6.5 ± 1.10	6.2 ± 0.67	8	3
5	20	5.7 ± 1.10	5.7 ± 1.10	9	5
13	139	11.2 ± 3.75	7.3 ± 1.76	24	12[b]
15	17	7.0 ± 0.58	3.0 ± 0.00	4	2
16	16	10.7 ± 3.98	4.3 ± 2.25	7	4
18	20	12.4 ± 1.60	9.0 ± 1.10	15	9
19	11	13.4 ± 5.07	5.2 ± 0.72	10	6
21[a]	20	5.4 ± 1.10	5.4 ± 1.10	7	3
22	18	4.9 ± 1.23	4.9 ± 1.23	11	8
25	14	9.0 ± 2.57	7.4 ± 2.10	16	12
27[a]	14	7.4 ± 2.82	6.9 ± 1.46	24	10
30[a]	20	8.6 ± 1.70	3.4 ± 0.94	4	6
Total	427	—	—	150	—

[a] Indicates a male that sang songs identical to one of its neighbors.

[b] Twenty songs used to make this measurement in order to standardize the number of song patterns found in 20 (or less, if few songs recorded) consecutive songs.

approximately ±15%, as there is at least this amount of variation within any one male's recorded songs; this variation is due to both the individual male and to recording artifacts, e.g., the changing distance of the animal from the microphone (Richards and Wiley, Am. Nat. 115:381–399, 1980).

A song figure was considered to be part of a song if it was separated from the other song figures by no more than 500 msec. Often males attached a call to their song, as a prefix; these calls were also given in non-song contexts. If the call was not separated from the main body of the song by more than 500 msec, it was considered to be part of the song, and was included in all song measurements.

Fourteen of 18 male orioles recorded provided sufficient numbers of songs for analysis (at least 10 songs/male of good acoustic quality, as judged by clarity and completeness of sonagrams). The remaining four males are included here, even though only a few songs were recorded for each, because each sang songs identical to one of the other 14 (see below). Sonagrams of 427 songs were used to measure song characteristics of the 14 male orioles. For 12 of these males, sonagrams of 20 consecutive songs/male, or less if fewer songs were recorded, were prepared (Table 1). Males 1 and 13, for which more songs were recorded, had five groups of 20 consecutive songs and eight groups of 20 consecutive songs analyzed, respectively. Additional sonagrams were made to examine the sequences of songs sung by males 1 and 13.

Mean song rates were determined for males 1 and 13 by averaging their song rates over several 10-min taped periods. Intervals between songs were measured directly from tape recordings, using a stopwatch.

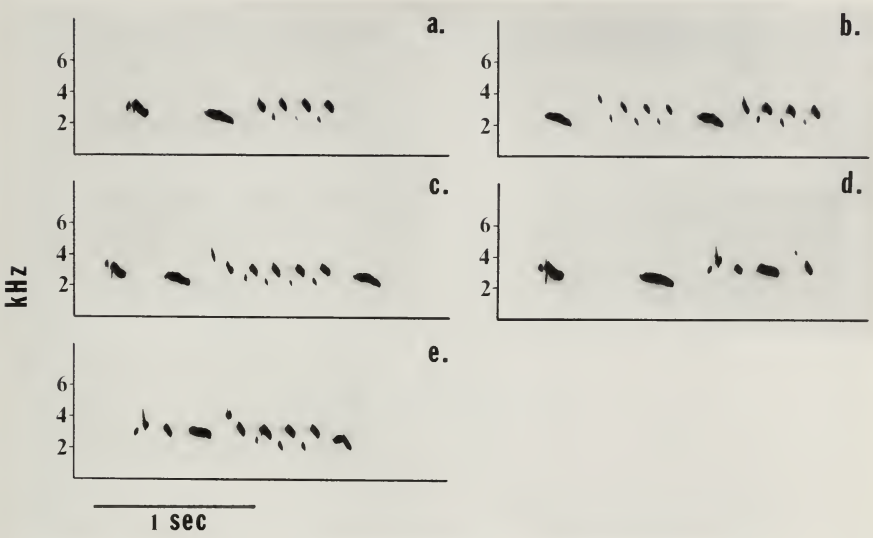


FIG. 1. Five of the song patterns sung by male 13. The last seven song figures in (a) constitute a characterisitic grouping for male 13; the song patterns illustrated here differ mainly in the arrangement of this grouping, e.g., in (b) there are two of these groupings, in (c) the grouping is expanded (to nine figures) and the entire grouping is absent from (d).

Results.—Male oriole songs are composed of a series of short, discrete song figures, ranging in number from 4–20 ($\bar{x}$ = 8.5 ± 2.6, N = 427 songs). Each male sang several variations of his song, here called song patterns, which were composed of varying numbers and sequential combinations of figures. For example, the last seven song figures in Fig. 1a constitute a characteristic grouping for male 13; in the subsequent three sonagrams (Fig. 1b–d), this group of figures is modified or absent. For most males, the majority of their song patterns were quite similar and often only the addition, subtraction, or positional change of a single figure distinguished one song pattern from another. Based on 20 consecutive song samples, individual males possessed from 2–12 song patterns ($\bar{x}$ = 6.5 ± 3.4, N = 14 males, Table 2).

Male 1, with a repertoire of five figures (song figure repertoire = the total number of different figures found in all analyzed songs of a given male, ranging from 4–24, $\bar{x}$ = 10.7 ± 6.7, in 14 males, Table 2), sang nine different song patterns during one period of 100 consecutive songs. Male 13, with 24 song figures in its repertoire, sang 42 different song patterns during a similar period (Fig. 2). There was a positive correlation (r = 0.80, $P < 0.01$, N = 14) between the figure repertoire size and the number of song patterns sung by each male.

Ten of the 18 males sang unique sets of song patterns (e.g., Fig. 3a–g). Four pairs of males possessed at least some song patterns that were identical. It was not possible to record enough songs for each of these pairs to determine if complete song pattern repertoires were identical, but they did appear to possess identical figure repertoires. Males with identical songs had adjacent territories; however, eight of the remaining 10 males (four pairs) occupied adjacent territories and did not sing identical songs.

Song figures varied in morphology (many quite simple, others complex), frequency range

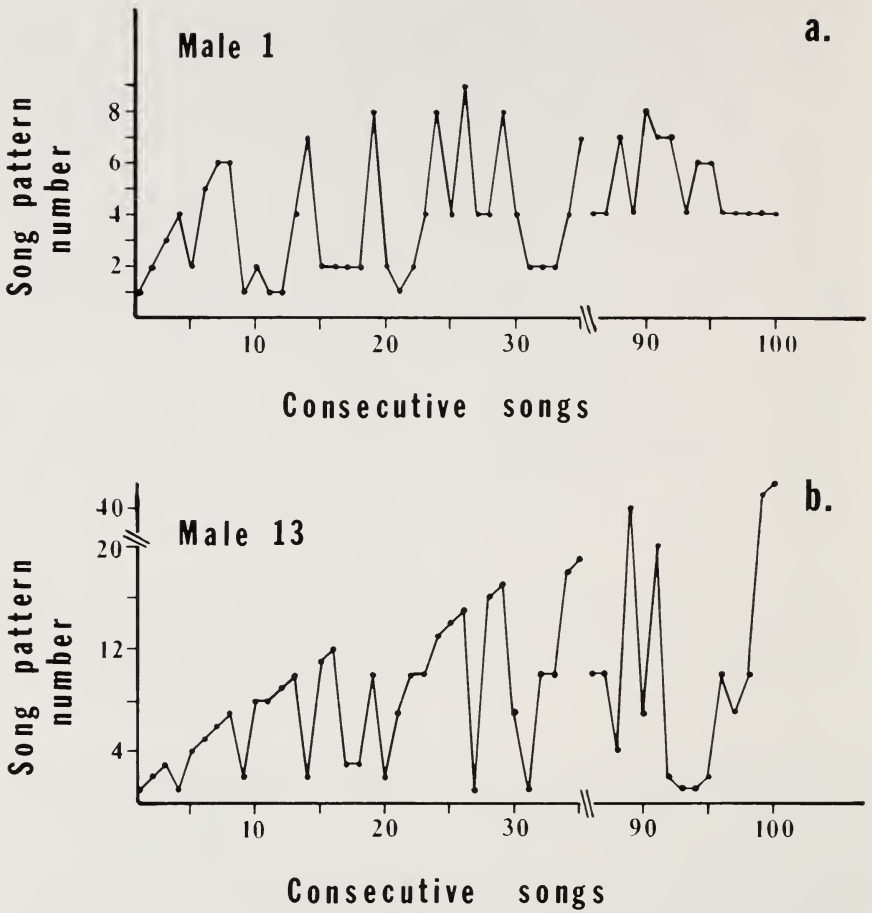


FIG. 2. (a) Song pattern sequence used by male 1 during a singing period of 100 consecutive songs; (b) song pattern sequence used by male 13 during a singing period of 100 consecutive songs. Note: different song patterns were consecutively numbered, starting with one, for each male; hence, song pattern two for male 1, for example, is not the same as song pattern two for male 13.

(some figures almost pure tones, others modulated in frequency over the entire bandwidth of the song) and duration (from 30–230 msec, $\bar{x} = 107 \pm 52$ msec). One hundred fifty different song figures were distinguished from the 427 songs of the 14 males. Of these, only three figures were found in the figure repertoires of more than one male and in each of these cases only two males shared the same figure. Adding the figure repertoires of the four identical-song males, bringing the sample size to 18 males, a total of 44 song figures, or 29% of the 150 known figures, were shared by at least two males.

All male orioles used similar frequency spectra in their songs (Table 1). The frequency

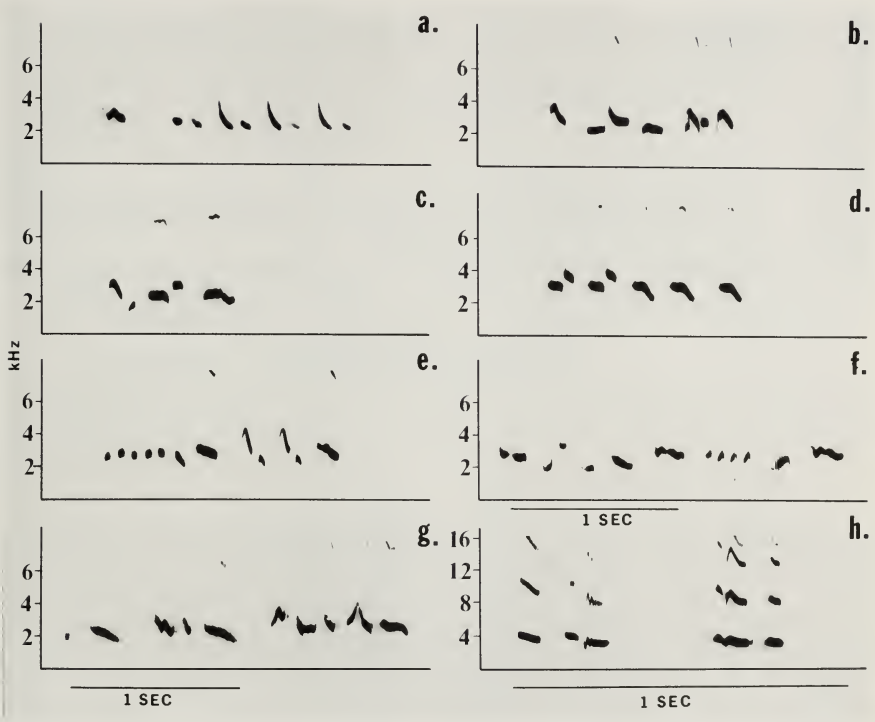


FIG. 3. (a–g) Song patterns sung by seven male orioles from the same population, illustrating differences between males. Only one song pattern for each male is shown. (h) Sonagram of a song illustrating the harmonic sturcture of male oriole song.

ranges of a male's song patterns were usually the same, as many of the song patterns consisted of the same song figures in different orders. The mean frequency range for all 427 songs analyzed was 2.1 kHz. The mean low frequency was 1.8 kHz; the mean high frequency was 3.9 kHz. Harmonics were found to be characteristic of many of the orioles' songs (Fig. 3h).

Oriole songs had a mean duration of approximately 1.4 sec. Certain males sang relatively short songs, consisting of from four to six figures; mean song durations for these males were less than 1 sec (Table 1). Other males sang songs that averaged over 2 sec in duration and routinely consisted of 12–14 figures.

Singing was not organized into "bouts" as described for various other species such as Cardinals (*Cardinalis cardinalis*) (Lemon, Behaviour 32:158–177, 1968) and Indigo Buntings (*Passerina cyanea*) (Thompson, Z. Tierpsychol. 31:39–59, 1972). Before the females arrived on territories, the males sang almost incessantly during the morning hours, at times singing series of songs separated by intervals as brief as 4 sec (e.g., male 13, Fig. 4a). After pairing of males and females occurred, mean intervals between songs increased (Fig. 4b). In the case of males 1 and 13, song rates progressively decreased during the remainder of the breeding season (Fig. 5).

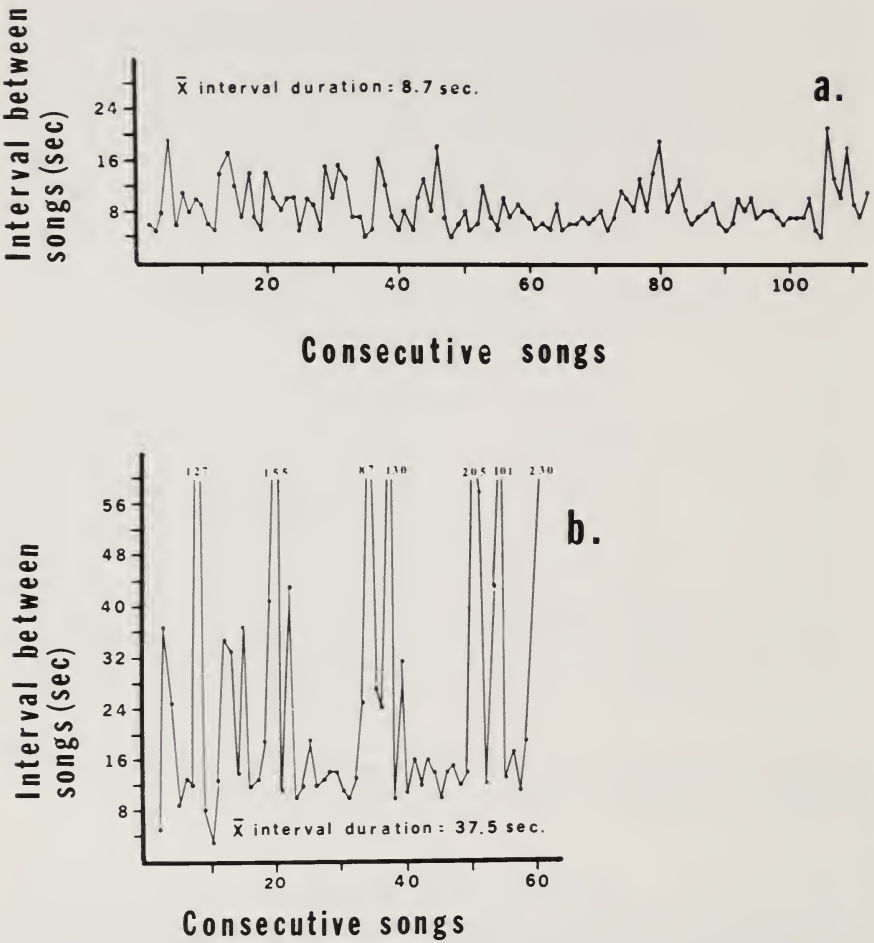


FIG. 4. (a) Intervals between songs for male 13 before the arrival of a female on his territory; (b) intervals between songs for male 13 after female arrival.

Sequences of song patterns sung by male orioles did not follow any regular pattern (Fig. 2a,b), as has been reported for Fox Sparrows (*Passerella iliaca*) (Martin, Condor 79:209–221. 1977) and several species of wrens (Kroodsma, Am. Nat. 111:995–1008, 1977), nor did the orioles sing each of their song patterns before repeating one, as in Western Meadowlarks (Falls and Krebs, Can. J. Zool. 53:1165–1178, 1975). Instead, a less ordered arrangement of consecutive song patterns exists; however, at least in the one case which lends itself to statistical analysis, the arrangement of consecutive songs is not random (Kolmogorov-Smirnov test for goodness-of-fit for the 99 song pattern transitions from male 1, Fig. 2a, Table 3; $P < 0.05$). Some song patterns were uttered more frequently than others (e.g., male 1,

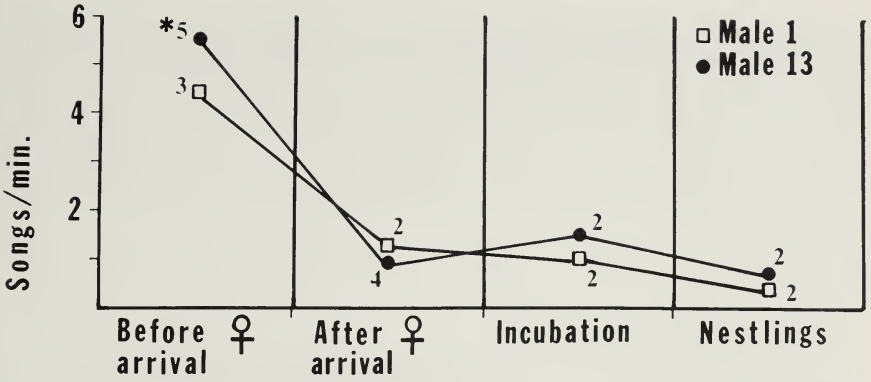


FIG. 5. Song rates for two male orioles during the course of the breeding season. *Note: These numbers refer to the number of 10-min periods used to compute the song rate data points.

patterns 2, 4, Fig. 2a), and some patterns were repeated consecutively (e.g., pattern 4, Fig. 2a). The average intervals between consecutive similar song patterns (14 ± 15.1 sec, N = 41) and consecutive different song patterns (14 ± 11.6 sec, N = 157) for males 1 and 13 (data pooled from Fig. 2) were alike ($P > 0.05$, t-test of the equality of two means).

Males each possessed several different short calls (Fig. 6a–e) and a "chatter" call of variable length. The short calls varied extensively in duration (23–227 msec), but all used the same general frequency range (1.5–3.7 kHz). As much of the males' behavior was obscured by foliage, and as these calls were often difficult to distinguish in the field, the assignment of specific functions to these short calls on a contextual basis was impossible. Short calls were usually interspersed between songs and frequently incorporated into the

TABLE 3

SONG PATTERN TRANSITIONS FOR 100 CONSECUTIVE SONGS FROM MALE 1[a]

Preceding song pattern	Following song pattern									Total no. songs
	1	2	3	4	5	6	7	8	9	
1	1	3	0	1	0	1	0	0	0	6
2	2	5	1	2	1	1	4	1	0	17
3	0	0	0	1	0	0	0	0	0	1
4	1	3	0	24	0	6	4	4	0	42
5	0	0	0	0	0	1	0	0	0	1
6	1	2	0	5	0	3	2	0	1	14
7	0	3	0	6	0	2	1	0	0	12
8	0	1	0	3	0	0	1	0	0	5
9	0	0	0	1	0	0	0	0	0	1
Total	—	—	—	—	—	—	—	—	—	99

[a] These 100 song patterns correspond to the graph in Fig. 2a.

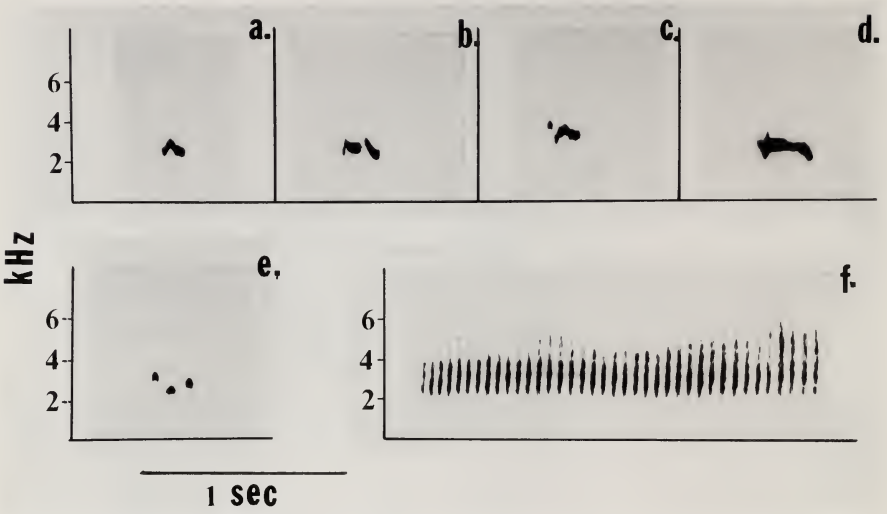


FIG. 6. (a–e) Male oriole "short" calls; (f) male oriole "chatter" call.

songs; in the latter case, calls served as song prefixes or appeared in other parts of the song. Twenty-six percent of the songs analyzed for male 1 included a call figure; similarly, 58% of the songs from male 13 contained call figures.

Chatter calls consisted of up to 38 repetitions of the same call figure (N = 62 chatter calls from 14 males). Individual chatter figures varied from 23–69 msec, with all figures in a given chatter call being of fairly uniform duration, and frequencies used extended from below 1.5 kHz to above 6.5 kHz (Fig. 6f). Each male produced chatter calls of different durations. For example, 17 chatter calls were recorded from male 13 including calls of 3, 4, 6, 7, 8, 9, 10, 18, and 20 figure repetitions. "Chatter" was given during male–male agonistic encounters, during interspecific chases by the male and during human intrusion into the territory, suggesting a possible general agonistic function for this call. Males also gave chatter calls as they approached females and/or nestlings when they brought food to the nest. Females possessed similar chatter calls and uttered them in agonistic situations (Beletsky, unpubl. data).

Discussion.—The songs of most males in the present study differed markedly in mean duration, and in the number and types of song figures used. Similar patterns of variation, in which the songs of few or none of the males in a population are similar, have been found in such species as eastern populations of Rufous-sided Towhees (*Pipilo erythrophthalmus*) (Borror, Condor 77:183–195, 1975; Ewert, Anim. Behav. 28:379–386, 1980) and Common Yellowthroats (*Geothylpis trichas*) (Borror, Living Bird 6:141–161, 1967; Wunderle, Auk 95: 389–395, 1978).

While the songs of most male orioles differed, some males sang identical songs; this observation is worthy of consideration. Among 18 males, four pairs of male orioles (the members of each pair holding adjacent territories) sang identical songs. One possible explanation for this phenomenon is that some males, during the first spring they establish territories, adjust their songs to those of their neighbors, as has been described for Indigo Buntings (Thompson, Auk 87:58–71, 1970) and Canaries (*Serinus canaria*) (Güttinger, Z. Tierpsychol.

49:285–303, 1979). Alternate explanations are that the identical song males are either: (1) parent-offspring pairs, in which case the male offspring learn their songs from their fathers, or (2) siblings or unrelated males reared in the same locality, learning their songs from the same adult male, returning to the same area to breed, establishing adjacent territories and singing identical songs. I do not possess enough data to comment on the possible validity of these hypotheses.

Acknowledgments.—I would like to thank the Huron-Clinton Metropolitan Authority for permission to work in Kensington Metropark, and W. L. Thompson, J. T. Armstrong, E. Shy, D. Ewert, D. Martin, J. W. Hardy, N. Flood and an anonymous reviewer for many helpful comments on earlier drafts of this manuscript.—L. David Beletsky, *Dept. Biological Sciences, Wayne State Univ., Detroit, Michigan 48202. Accepted 5 Jan. 1982.*

Wilson Bull., 94(3), 1982, pp. 381–385

Documentation and status of Cory's Shearwater in the western Gulf of Mexico.—Cory's Shearwater (*Puffinus diomedea*) has only been reported in the western Gulf of Mexico (W of longitude 94°) since 1975, when several birds were observed and one photographed about 64 km ESE from Port Aransas, Texas, by Scott Holt (Univ. Texas Marine Lab., pers. comm.) on 6 September 1975. Prior to this, the only published record for the entire Gulf of Mexico proper was a sighting off the Alabama coast in September 1973 (Imhof, Alabama Birds, 2nd ed., Univ. Alabama Press, Alabama, 1976; Duncan and Havard, Am. Birds 34: 123, 1980). Although Murphy (Serial Atlas of the Marine Environment: Distribution of North Atlantic Birds, Am. Geogr. Soc., 1967) listed four specimens taken from the Cuban Straits off the Florida Keys, there is no documented specimen for the Gulf proper.

Specimen description.—On 12 August 1980, I found a dead female Cory's Shearwater (Univ. Dallas collection No. 2575) washed ashore on Mustang Island, 6 km S of Port Aransas, Nueces Co., Texas. This was 2 days after the passage of Hurricane Allen through the western Gulf and 96 km N of where the eye of the storm made landfall on the south Texas coast. Other pelagic species found dead the same day and within 2 km of the shearwater included three Sooty Terns (*Sterna fuscata*) and an Audubon's Shearwater (*P. lherminieri*). The previous day a dead Manx Shearwater (*P. puffinus*) (most unusual) and Brown Booby (*Sula leucogaster*) were found in this area (Webster, Am. Birds 35:201–204, 1981). No other Cory's Shearwater was encountered during this time.

The specimen was preserved as a study skin and subsequently identified as *P. d. diomedea* (Mediterranean race) by George E. Watson of the National Museum of Natural History, Washington, D.C. The plumage exhibited signs of extensive molt and heavy wear, with the feather bases showing especially on the secondaries and "rump." The condition of the plumage and distance from the Mediterranean at that time of year are evidence that the bird was an immature, prebreeding individual, in agreement with Forsythe (Wilson Bull. 92:265–266, 1980; specimen off South Carolina in July 1973) and Jouanin et al. (Oiseau 47:351–358, 1977; banded specimens of the eastern Atlantic race, *P. d. borealis*, recovered off Rhode Island and in the Atlantic Ocean away from their nesting grounds). The present specimen and previous western Atlantic specimen records (Murphy 1967, Jouanin et al. 1977, Forsythe 1980) suggest that the smaller Mediterranean subspecies may be more regular in southern U.S. waters compared to the *borealis* subspecies.

Distribution in the western Gulf.—Numerous cruises since 1975 in the western Gulf have

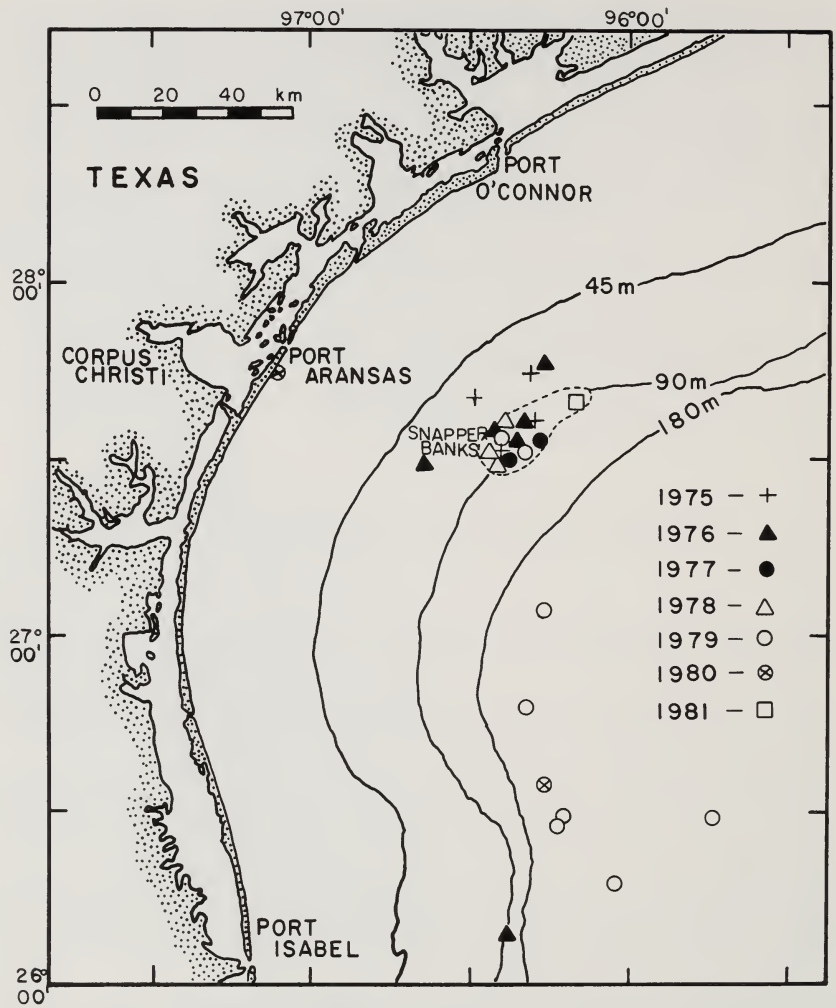


FIG. 1. Map of South Texas Offshore Continental Shelf, showing locations of Cory's Shearwater sightings over 1975–1981 in relation to water depth and distance offshore.

produced at least 24 sightings of Cory's Shearwater (Fig. 1). Coverage of the south Texas continental shelf was achieved from 1975–1978 in conjunction with monthly or trimonthly surveys by the Univ. Texas Marine Science Institute (MSI) for the Bureau of Land Management, Dept. Interior. Since 1975, Texas birders have regularly visited offshore fishing banks out of Port Aransas and Galveston, during many months of the year (see Am. Birds reports from 1976–1981). In 1979, staff from MSI again made extensive cruises over the western Gulf shelf to study the distribution of oil spilled from the Mexican oil well, IXTOC–1 (Amos, Ixtoc Oil Spill Rept., unpubl., Univ. Texas Mar. Sci. Inst., Port Aransas, Texas, 1980). In

1979 and 1980, U.S. Fish and Wildlife personnel made 12 aerial surveys of south Texas shelf water, which yielded significant sightings of Cory's Shearwaters (Hoffman et al., Northeast Gulf Sci. 5:55–57, 1981).

From the incidence of records Cory's Shearwater is the singularly most abundant and regularly-occurring shearwater species in the western Gulf during the summer–fall season. This is most surprising in view of the fact that Audubon's Shearwater nests much closer to this area (in the West Indies and Bahamas), and that the Greater Shearwater (*P. gravis*) also migrates in numbers along a route out in the western Atlantic similar to that of *P. diomedea* (see Murphy 1967). However, the Greater Shearwater has been reported in the western Gulf only three times in the entire 10-year period 1970–1980 (Arnold, Auk 92:394–395, 1975; Webster, Am. Birds 30:1125, 1976; Pulich, pers. obs.). Audubon's have been seen only about 10 times off the Texas coast during 1970–1980 (Duncan and Havard 1980; Pulich, specimen, 1980; Webster 1981; J. Bird, Univ. Texas MSI, pers. comm.). Moreover, neither species has been observed in large flocks like Cory's.

All reports of live Cory's Shearwaters have been from more than 50 km offshore, with the largest concentrations occurring on the outer continental shelf, 70–100 km out. The "Snapper Banks" (deep water rock formations) offshore from Port Aransas (Fig. 1) are now well known as sites where the species can predictably be found in season. On a trans-Gulf cruise from Port Aransas to Key West, Florida, I saw no Cory's Shearwaters between 28 September and 2 October 1978. However, between 19 August and 21 October, birders reported the species on several occasions at the Port Aransas Snapper Banks (Webster, Am. Birds 33:193–195, 1979).

Dates of occurrence for the western Gulf range from 26 June 1980 (Hoffman et al. 1981) to 10 November 1976 (Holt, pers. comm.). The seasonal peak has generally been in late September–early October (30+ birds, pers. obs.; 45+ birds, Webster, Am. Birds 31:197–199, 1977). However, between 20–22 August 1979, when IXTOC-1 oil was floating northwards towards the south Texas coast from the Bay of Campeche, Mexico, 150–200 Cory's Shearwaters were reported in association with pelagic fishes, sharks, dolphins and pilot whales (*Globicephala macrorhynca*), about 100 km E of South Padre Island, Texas, by Hoffman et al. (1981).

Hydrographic data collected during a 1976 cruise suggest a relationship between Cory's Shearwater distribution and water mass boundaries over the south Texas continental shelf. Over the period 10–16 September 1976, surface water salinities and temperatures showed the patterns in Fig. 2 (taken from Smith, pp. 53–75 *in* Chemical and Biological Survey of the South Texas Outer Continental Shelf, Third Quart. Rept. to Bur. Land Manage., Contract No. 08550-CT6-17, unpubl., Univ. Texas Marine Lab, Port Aransas, Texas, 1976). As noted in this figure, shearwaters were seen only near boundary areas between 36‰ and 35‰ water masses, while there was no obvious correlation with water temperature. Such boundary regions (fronts) between water masses of different densities are highly productive elsewhere for pelagic organisms (e.g., Patagonian Shelf off Argentina, Labrador Current off Canada; see Brown, pp. 1–39 *in* Behavior of Marine Animals, Vol. 4, J. Burger, B. Olla, and H. E. Winn, eds., Plenum Press, New York, New York, 1980). Similarly, the western Gulf continental shelf break could attract Cory's Shearwaters, in addition to the schools of pelagic fishes (e.g., tuna and mackerel) known to concentrate there (Hoffman et al. 1981).

Discussion.—Bourne (pp. 155–160 *in* Handbook of North American Birds, Vol. 1, R. S. Palmer, ed., Yale Univ. Press, New Haven, Connecticut, 1962) states that large numbers of *P. d. diomedea* and *P. d. borealis* cross the Atlantic in mid-summer, then move up the northeastern United States coast in fall, and congregate off New England and the Canadian maritime region (see Murphy 1967; Finch et al., Am. Birds 32:152, 1978) before returning to the eastern Atlantic in winter. The information herein demonstrates how Cory's Shearwaters

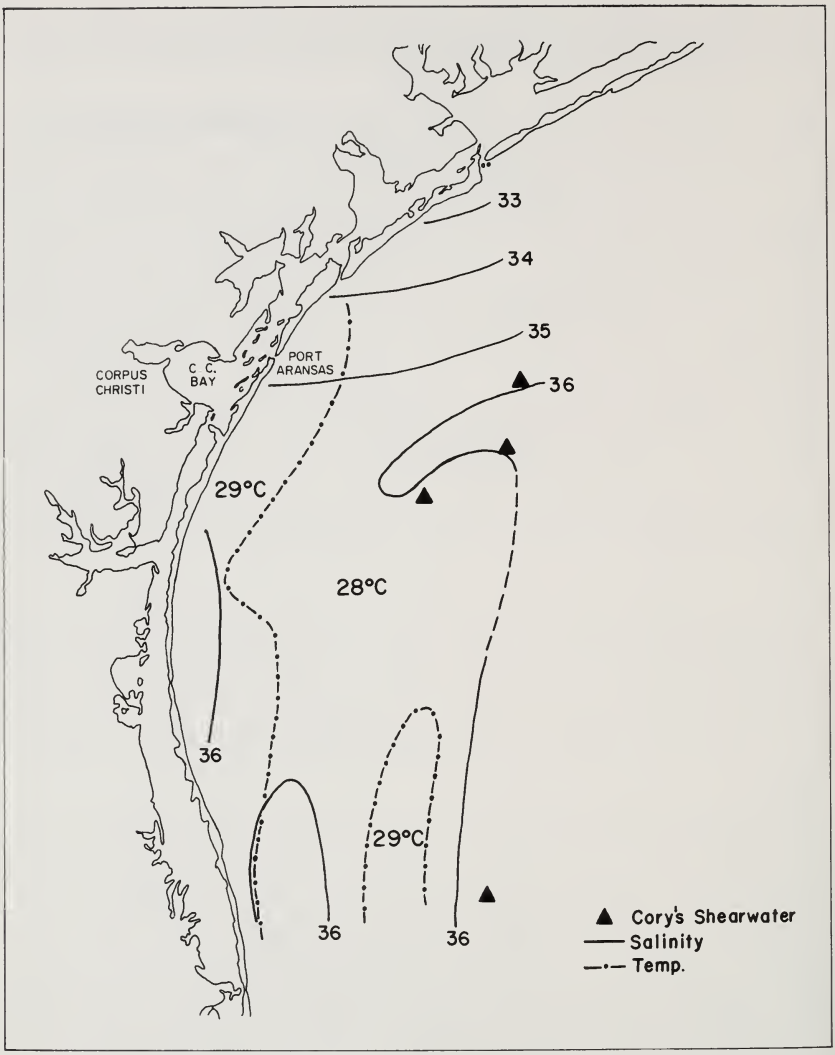


FIG. 2. Distribution of Cory's Shearwaters over South Texas Continental Shelf from 10–16 September 1976 in relationship to salinity and temperature of surface waters.

also regularly move into the western Gulf of Mexico during summer–autumn, in sharp contrast to other procellariids.

These observations provide further insight into the life history and ecology of this Atlantic Basin shearwater. Jouanin et al. (1977) had speculated that Cory's Shearwaters (from one particular colony of the *borealis* race) spent their first 5 years wandering the open ocean (north and south Atlantic), since banded nestlings did not return to their nesting grounds

until 5 years old and breeding did not occur until the birds were 6 years old. The congregating of these prebreeding wanderers in a remote, but specific, Gulf of Mexico pelagic zone illustrates how closely their distribution on the high seas is tied to their warm-water life cycle. The eco-physiological factors which regulate their dispersion over the high seas appear most intriguing when the routes taken by wandering Cory's Shearwaters are considered, such that some enter the Gulf of Mexico and others travel the Gulf Stream up the eastern U.S. coast.

Acknowledgments.—I thank A. W. O'Neil of Falfurrias and Ray Little of Portland, for information on pelagic birding trips. I am especially grateful to the following: Scott Holt (who first reported these birds in 1975), Jerry Bird, and Anthony Amos of Univ. Texas MSI, for kindly providing data on pelagic observations and for stimulating discussions; the late Eugene Eisenmann for comments on plumage of Cory's Shearwater; Warren Pulich, Sr., who preserved and examined the specimen and commented on an early draft of the manuscript; George E. Watson, for his subspecific identification of the specimen; Dennis Forsythe who reviewed the manuscript and provided significant reference material; and Jon Barlow, whose editorial review greatly improved the final manuscript. The Univ. Texas Marine Science Institute supported this work and provided ship time. This is contribution No. 509 of the University of Texas Marine Science Institute.—Warren Pulich, Jr., *Univ. Texas Marine Science Institute, Port Aransas, Texas 78373.* *Accepted 15 Sept. 1981.*

Wilson Bull., 94(3), 1982, pp. 386–392

ORNITHOLOGICAL LITERATURE

CONSERVATION OF NEW WORLD PARROTS. By Roger F. Pasquier (ed.). Smithsonian Institution Press, 1981:485 pp., text figs. and tables. $14.00.—The Parrot Working Group of the International Council for Bird Preservation was formed in Canberra, Australia, in 1974. In view of the particular concern for parrots of the Caribbean, their second meeting, in 1980, was held on St. Lucia. The proceedings of this assembly are published in this volume. As such, the book is not only a comprehensive and up-to-date account of the status of many New World parrot species, but includes a fair amount of information on parrot aviculture, natural history, and behavior.

From one paper after another there emerges a rather grim outlook for many New World parrot populations. Most of their problems are those common to wildlife in rainforest ecosystems. Habitat destruction due to human influences has greatly accelerated in recent years. Agricultural and mineral concerns have subjected vast areas to slash and burn techniques, destroying food sources and suitable nesting sites. The latter is particularly a problem for parrots, since many species require a relatively large core area and nest in large, hollow trees. Also, farmers in these areas shoot parrots as indiscriminately as they do any animal that appears to take a toll on their crops.

But parrots have another problem, unique to their order, and possibly as devastating as any of these habitat alterations. They hold an incredible, indeed (in view of current parrot prices) irrational appeal to humans. The occasional pet parrot kept in areas within their normal range has probably never significantly decreased their populations, but the current pet trade is harvesting and exporting them in such numbers that populations are being seriously threatened. Moreover, their methods of collecting and maintaining the birds are so sloppy that a large percentage never make it to market.

It is pointed out in the book that many of these countries have passed laws forbidding collection or export of parrots. Enforcement of these laws, however, is another matter. It is not at all uncommon for a parrot to retail in the United States for over $2000. While this hardly rivals the profits to be had in drugs, it's not bad, and the penalties for getting caught are proportionately lower. Consider, for example, the profit to be made on a bird such as the Indigo Macaw (*Anodorhynchus leari*), whose home was recently discovered by Helmut Sick. His reluctance to reveal the locality was overcome by his faith in the Brazilian government's ability to enforce laws forbidding the collection of this bird in at least part of its range. Although I hope he is correct, I suspect he may have created a serious problem for this previously undisturbed species.

The very fact that this meeting took place, and that this book was published does provide a positive note for parrot conservation. Obviously some people are concerned, and attempts are being made to correct bad situations, as well as to prevent similar problems in less perturbed areas. Numerous breeding programs are described. These are not aimed at satisfying pet hunters. The general tone of the papers given here deplores the keeping of parrots for reasons other than reestablishment of wild populations. The accounts of natural history and ecology are aimed at providing information to help such breeding programs. Finally, and ironically, I believe that the outbreak of Newcastle disease in the United States during the last decade may ultimately be beneficial to parrots, owing to the resulting import regulations and their enforcement.

From the standpoint of biology libraries the book has two shortcomings. One is its very specialized nature. Even within the realm of ornithology it will probably have limited appeal. In fact, even some parrot specialists might not consider it essential for their libraries. The other problem is its very timely nature. The status of these populations is dynamic, and what

is useful information at this time will require updating a decade from now. Thus, I recommend this book for libraries of large institutions, with ample book-purchasing budgets, and for libraries of individuals interested in this particular problem at this particular time.—Susan L. Berman.

Animal Migration. Society for Experimental Biology Seminar Series 13. By D. J. Aidley (ed.). Cambridge University Press, Cambridge, United Kingdom, 1981:264 pp., 92 numbered text figures, 19 tables. $39.95 (hard cover), $19.95 (paper cover).—This volume is one of the few that attempts to tie together the wide variety of current studies on animal migration. It contains the proceedings of the 1979 Society for Experimental Biology Seminar Series Symposium on Animal Migration. As an introductory review for the general biologist it is not a highly technical work, and is designed to highlight the wide range of contemporary studies in animal migration without being comprehensive. A research-oriented approach is used to present ideas, empirical evidence, and possible directions for future research. Ecological aspects of migration are stressed rather than the more common behavioral treatments.

There are 12 chapters, each by a different contributor. The first chapter, by D. J. Aidley, discusses some of the questions, problems, and hypotheses in the study of animal migration. The remaining chapters discuss the migratory movements of insects, fishes, birds, whales, and humans. One of the outstanding contributions, and one of his last, is that of the late W. T. Keeton, who provides a superb explanation of the contemporary hypotheses and research techniques of avian orientational and navigational mechanisms. He presents evidence for both the more familiar orientation cues (e.g., celestial), and the unusual sensory capabilities of birds, including detection of barometric pressure, infrasound, polarized light, ultraviolet light, and olfactory cues, and possible detection of magnetic cues and gravity variations. Keeton also discusses conflicts within the field of avian orientation and navigation.

Contributions from T. Alerstam, G. P. Arnold, F. R. Harden Jones, and T. R. E. Southwood are particularly noteworthy. Alerstam examines "The course and timing of bird migration," emphasizing avian migratory strategies for dealing with various weather parameters. Though this chapter is technical, Alerstam integrates his topic in a clear and concise manner.

G. P. Arnold and F. R. Harden Jones deal with the movements of fish. Arnold presents a hypothesis for the migratory movements of North Sea plaice that relies on differential drift in tidal currents, termed "selective tidal stream transport." Harden Jones also discusses this concept, as well as pelagic fish migration based on ocean current transport and olfactory navigation.

T. R. E. Southwood's chapter, "Ecological aspects of insect migration," though short, is particularly interesting in that it presents animal migration from the insect's perspective. Southwood compares migratory strategies between phyla, demonstrating major similarities as well as differences. It is perhaps this chapter, more than any other, that unifies the book.

Though the principal emphasis of the work is on basic research, two chapters discuss applied aspects of animal migration. R. J. V. Joyce presents an insect pest control management scheme that takes into account insect mobility, resulting in increased economy of human resources, control of insects, and decreased crop damage. G. V. T. Mathews discusses international policy on migrant bird conservation.

In the final chapter, "Man and other vertebrates: a common perspective to migration and navigation," R. R. Baker presents the new and highly controversial hypotheses that (1) migratory behavior is an extension of exploratory behavior, and (2) humans are able to sense and use the geomagnetic field for orientation.

Of the 12 authors contributing to this volume, 10 were from the United Kingdom; thus, the scope of ideas and supporting references are slightly narrower than if more scientists had been invited from other countries. Overall, however, this book has attained its goal of providing an overview of animal migration for the general biologist. The synthesis of material makes a positive contribution to the scientific literature, and I recommend this volume to any biologist interested in animal migration.—HUGH MCISAAC.

OSMOREGULATION IN BIRDS. By Erik Skadhauge. Springer-Verlag, Berlin, West Germany, 1981:x + 203 pp., a few black-and-white photos and drawings, numerous figs. and tables. $52.50 (cloth).—This is Volume 12 in the series Zoophysiology (formerly Zoophysiology and Ecology) from Springer-Verlag. Erik Skadhauge has prepared a thoroughly physiological, organ-based treatment of osmoregulatory processes in birds. Each chapter treats a separate organ and its function (although separate chapters are devoted to Uptake from the Gut and Function of the Cloaca); additional chapters are devoted to the interactions of excretory organs, a survey of hormones and osmoregulation, and the special problems of desert life, migration, and egg-laying.

Generally, each chapter (and some major passages) is introduced with a precis of highlights to come, and a short summary statement completes the chapter. Overall treatment is thorough, well-balanced and properly documented by adequate citation. In many areas where controversy or inadequate literature exist, shortcomings are clearly outlined and analyzed, and directions for future research are presented. Many chapters contain large tables which summarize pertinent data; figures reproduced from the original literature are used abundantly. A nice touch appears at the end of the last chapter—notes added in proof are included for each chapter, with citations to papers published up to the end of 1980. The sources of these papers are included at the end of the extensive list of references. The volume also contains a systematic and species index, and a skimpy subject index.

Although the book is expensive, it is well- and attractively-made. However, numerous spelling or typographic errors prove irksome and detract from the otherwise high quality of the book. For no apparent reason, two types of paper have been used for the pages.

Overall, this volume represents a valuable source book for anyone interested in comparative aspects of avian osmoregulation, but requires a reasonable grounding in animal physiology to be fully accessible to the reader. I recommend it to researchers interested in avian physiology, and to graduate students already versed in comparative physiology.—ROGER A. MCNABB.

THE WADING BIRDS OF NORTH AMERICA (NORTH OF MEXICO). By Allan W. Eckert. Illus. by Karl Karalus. Doubleday & Co., Inc., Garden City, New York, 1981:252 pp., 32 color plates and species sketches. $49.95.—As children we are taught, "If you have nothing nice to say, don't say anything at all." This maxim was probably not meant for book reviewers, who also have responsibilities to notify or warn potential purchasers. But it portends a short review to come. If you typically read only the first paragraph of reviews, you just saved $49.95.

The book's intended purpose is hard to discern (e.g., no mention of it in the Introduction). Pretentious dust-jacket claims notwithstanding, this is not "a definitive work on the wading birds." It does not extend our knowledge of the species covered, nor does it unite disparate literature in new and useful ways. On the other hand, it is large, colorful, and expensive, all of which suggest that it was intended as a coffee-table picture book. This impression is not undermined by the Introduction, which is devoted to a tedious disclaimer of responsibility

for why each subspecies was included or not. The Introduction also contains a few line drawings to orient the reader morphologically to such features as "toes," "rump," and "back" of a night-heron. It is obvious that the book is not aimed at professional or sophisticated amateur ornithologists.

The great bulk of the book (96% of the pages) consists of the individual subspecies accounts, which are followed by a pathetic three-page Bibliography and an Index. The taxonomic coverage is curious, including all U.S. and Canadian birds that wade except for those belonging to the Charadriiformes. I have never quite understood how this "American" definition of wading bird came to be so different from the "British" usage (which refers only to sandpipers et al.), but here it is again. This book has all our herons, ibises, cranes, rails, gallinules, and assorted relatives (spoonbill, stork, limpkin). Within families, taxonomic order is not followed: the book starts with *Butorides*, then *Nycticorax*, *Nyctanassa*, *Ardea*, *Florida*, etc.

Each subspecies is treated with some or all of the following separate headings: common name; scientific name; other or colloquial names; shape at rest and in flight; length and wingspan; beak; legs, feet, and claws; crests, plumage, annual molt; voice; sexual differences in size, coloration, and voice; coloration and markings—adult; coloration and markings—juvenile; general habits and characteristics; habitat and roosting; enemies and defenses; food and feeding habits; courtship and mating; nest and nesting habits; eggs and incubation; young; migration; and economic influence. This is a lot of information, but there are so many inaccuracies (contra the dust-jacket promise of "scientifically accurate descriptions") that the novel tidbits, which are extremely scarce anyway, are hard to trust. If many of the facts I know are misrepresented, how can I believe the new material? (Especially when none of it is cross-referenced. . . .)

For example of content and tone, I quote from the description of Eastern Green Heron courtship: "*Butorides striatus virescens* will prance and dance in the most outlandish manner at times . . . . Most often it appears to be doing this for its own amusement, but such is not the case . . . . A fascinating display, but oddly graceless and appearing rather awkward and ridiculous . . . ." This, the only display described, bears no resemblance to any I have seen in the field nor to the many analyzed in detail by Andrew J. Meyerriecks, whose classic ethogram (Nuttall Ornithol. Publ. No. 2, 1960) of Green Heron courtship is a cornerstone of the heron literature. This makes Eckert's next claim, that "other courtship activities are not well documented," even more revealing. The complete neglect of Meyerriecks' many heron papers clearly suggests that the author did not do his homework.

The lack of documentation for facts makes the whole book useless as a reference. The reader is supplied with quantitative nonsense, such as a breakdown of Green Heron diet as 40% fish, 30% insect, 24% crustacean, and 6% miscellaneous. Was this from one bird? Many stomachs? Over the whole range? But the author goes on to assume that Green Herons exert a significant effect on reducing populations of harmful insects (apparently from these diet data alone) in the Economic Influence section.

I think it safe to say that the two-decades-old Handbook of North American Birds, Vol. 1 (R. S. Palmer, ed., 1960) contains all the reliable information found in this book and is much more usefully documented.

The artwork, by Karl E. Karalus, is unremarkable. The dust-jacket's promise of perfect accuracy in all aspects is violated early and often (e.g., the Reddish Egret (*Egretta rufescens*) on Plate IX seems to have cherry-flavored neck plumage. The postures chosen are not interesting—e.g., virtually all are drawn in profile—and the colors are occasionally garish (e.g., the pink used for the flamingos). In the keenly competitive world of bird illustration, this book offers nothing unique.

In summary, I cannot recommend anyone spending $50 for this book. It is singularly

unlikely to live up to the dust-jacket's prediction that it "will soon become a treasured volume in the libraries of ornithologists and bird fanciers everywhere."—Douglas W. Mock.

Behavior of Marine Animals, Current Perspectives in Research, Volume 4: Marine Birds. By J. Burger, B. L. Olla, and H. E. Winn (eds.). Plenum Press, New York, New York, 1980:xvii + 515 pp., 78 figs., 47 tables, 2 appendices. $45.00.—This informative, loosely-knit flock of papers on the behavior and ecology of marine birds offers a multicolored view of these often dull-plumaged creatures. R. G. B. Brown begins with a chapter on the marine, non-breeding lives of these primarily terrestrial-nesting, colonial species. Sometimes effortlessly, sometimes laboriously, we then work our way through 10 additional chapters, which range widely in tone and substance from J. P. Ryder's terse, factual review of the influence of age on breeding biology to G. L. Hunt, Jr.'s, easy-reading and thought-provoking, theoretical discussion of mate selection and mating systems. B. M. Wenzel provides a valiant, yet frequently repetitive, effort to put our scanty knowledge of seabird chemoreception into a behavior-ecology perspective. F. G. Buckley and P. A. Buckley present a thorough review of habitat selection replete with something often needed in colonial bird research: rigorous definitions of terms. Definitions also highlight M. Gochfeld's comprehensive, occasionally redundant, mix of rigorous methodology, weak data (his own) and interesting theory on reproductive synchrony.

You can almost see a twinkle in the author's eye when you read C. G. Beer's articulate discourse on communication behavior and realize that his suggestion regarding animal cognition may be heretical to many humans. The twinkle may not be there, but R. M. Evans' comprehensive review of behavior development from an ecological viewpoint is nicely organized and to the point. Next, W. A. Montevecchi and J. M. Porter give an original account of parental feeding behavior by Northern Gannets (*Sula bassanus*) but unfortunately they fail to relate these data to theoretical questions as implied by the words "parental investments" in their title. A vast amount of information and erection of a conceptual framework stand out in J. Burger's very interesting, yet exceedingly long, treatment of fledgling independence and parental care. The book is capped by W. E. Southern's somewhat defensive, albeit knowledgeable, review of the distribution and orientation behavior of North American gulls.

Generally, this volume is a useful reference which provides valuable overviews of some major topics in seabird research. On the other hand, the different writing styles of the authors, the broad spectrum of approaches (e.g., review, theory, original data) and the endlessness of some chapters make the book seem unorganized and very tortuous reading as a whole. This appears to reflect a lack of constraints on authors which is further emphasized by the apparent absence of specific formats for the presentation of scientific names and citations as well as the lack of citations for statements that would normally require them. Typographical errors, including apparently missing chunks of text and inclusion of unnecessary and poor photographs, also suggest uncritical or limited editing. Although I would not call this book "invaluable" as the overleaf advertizes, I would recommend it to those who investigate the fascinating lives of marine birds.—Peter M. Fetterolf.

Saos Checklist of Southern African Birds. By P. A. Clancey, (ed.). South African Ornithological Society, Pretoria, South Africa, 1980:xiii + 325 pp., 26 maps. R15.—This checklist is the second edition of the South African Ornithological Society's official list of the birds of southern Africa, and appears only 11 years after the first edition. The reasons

for publishing this revised work so soon include: a need "to make available in a readily accessible form the large volume of recent systematic research, and, secondly, the amount of revisionary work which would have been required to update and correct the first edition was such that . . . an entirely new S.A.O.S. Checklist would in the end be simpler and more satisfactory."

The text covers Namibia, Botswana, Zimbabwe, Mozambique south of the Zambezi River, the Republic of South Africa, Lesotho, Swaziland, and their territorial waters. The nomenclature adheres to the principles of that laid down by the International Code of Nomenclature, 1961, and the systematic order follows Wetmore (1961), with some minor alterations "calculated to accommodate more recent thinking on the familial status of some taxa." This is basically a conservative checklist with few, if any, novel ideas set forth that would "disturb the overriding requirements of stability." However, the editor has not necessarily followed Peters' Checklist of the Birds of the World, e.g., *Andropadus* (Pycnonotidae) is retained.

The checklist includes all species and subspecies in southern Africa and gives the distribution of each. Frequently for subspecies no indication is given as to whether breeding, wintering or year-round range is being considered. This lack of specification of kind of range may simply be a reflection of our ignorance of specific natural history. Several distribution maps have been included to exemplify the range of the polytypic species. However, there is no explanation as to why maps are used for some species and not for others. A few of the maps are of sub-standard quality as portions look faded, with a concomitant loss of detail. The original reference is supplied for each family, genus, and subspecies.

A "Hypothetical List" has been included comprizing "species claimed for the southern African list solely on the basis of a sight record, unsupported by any unequivocal corroborative evidence, such as a clear photograph taken at the time, feathers, etc." A catalogue of "Fossil Records" at the end of the book tabulates all species now extinct in the region but known from fossil material found there.

An important feature of this work is the index to genera and to the English names used.

For the most part, this checklist has been very well compiled, and is a must for anyone interested in the most recent distributional and taxonomic account of the birds of southern Africa.—Willie Him.

Annotated Checklist of the Birds of Arizona, 2nd edition. By Gale Monson and Allan R. Phillips. University of Arizona Press, Tucson, Arizona, 1981:xxxi + 240 pp., 6 maps, paper cover. $5.95.—The status and distribution of 475 species of birds in Arizona are summarized in detail, enabling observers to more accurately identify birds seen in the field. This book, which is of a convenient size to carry in the field, is meant to be used in conjunction with a standard field guide. It does not contain illustrations of birds, but once they have been tentatively identified the detailed distributional and ecological information in this book will help to confirm identification, and should aid in compiling new information about each species' range and status. Every state should have a book like this.—R.J.R.

Birds of Oak Hammock Marsh Wildlife Management Area. By Kenneth A. Gardner. Manitoba Dept. Natural Resources, Winnipeg, Manitoba, 1981:172 pp., 14 pp. of color plates, numerous black-and-white photos, 3 maps, paper cover. $10.50 (Canadian).—This attractively printed book presents accounts of the distribution, status, and breeding of the birds of the area. Order from the Manitoba Museum of Man and Nature, Gift Shop, 190 Rupert Ave., Winnipeg, Manitoba R3B 0N2, Canada.—R.J.R.

Birds of Cattaraugus County New York. By Stephen W. Eaton. Bulletin of the Buffalo Society of Natural Sciences, Vol. 29, 1981:iv + 91 pp., 1 color plate, 4 maps, paper cover. $3.95.—The status and distribution of 262 species are reviewed for this county in western New York state. Most of the text is devoted to species accounts, but there are also sections on the geological and ecological conditions of the area. This book will be of primary interest to field observers in the region. Order from Gift Shop, Buffalo Museum of Science, Humboldt Parkway, Buffalo, New York 14211. Add $1.00 postage and handling. New York state residents add 7% sales tax.—R.J.R.

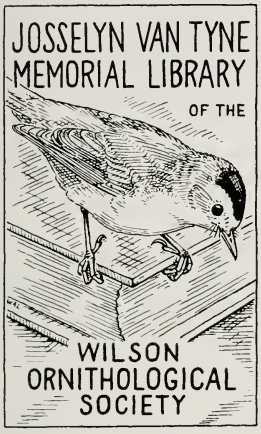
Alberta Naturalist, Special Issue No. 1. By Martin K. McNicholl (ed.). Federation of Alberta Naturalists, 1981:iv + 152 pp., numerous black-and-white photos, paper cover. $7.00 (Canadian). Alberta Naturalist, Special Issue No. 2. By Martin K. McNicholl (ed.). Federation of Alberta Naturalists, 1981:73 pp., numerous black-and-white photos, drawings, and maps; paper cover. $3.50 (Canadian).—The first of these publications contains a number of articles by different authors on the general topic of "The History of the Federation of Alberta Naturalists and its Corporate Member Clubs." The second is similarly organized around the subject of "Bird Banding in Alberta." They may be ordered from the Federation of Alberta Naturalists, Box 1472, Edmonton, Alberta T5J 2N5, Canada.—R.J.R.

Pheasants, their Breeding and Management. By K. C. R. Howman. K & R Books Ltd., Edlington, Lincolnshire, United Kingdom, 1979:117 pp., numerous color plates and black-and-white figs. £4.75. Quail, their Breeding and Management. By G. E. S. Robbins. World Pheasant Association, 1 Harraton Square, Church Lane, Exning, Suffolk CB8 7HA, United Kingdom, 1981:108 pp., numerous color and black-and-white figs. £6.95.—These attractively printed books aim to provide basic information on avicultural practices. They are similarly organized, including sections on aviaries, management, and husbandry; feeding, choice of species, breeding seasons, and importation. Each also includes a section reviewing the characteristics of the various species, including a collection of attractive color photographs or paintings of these often spectacular birds. There is also a brief discussion of the World Pheasant Association, which promotes the study and breeding of these forms.—R.J.R.

An annotated Bibliography of the Red-cockaded Woodpecker. By Jerome A. Jackson. Savannah River Ecology Laboratory, P.O. Drawer E, Aiken, South Carolina, 1981:290 pp. Price not given.—One-thousand-seven-hundred-ninety references are listed alphabetically by author and cross-referenced by subject and locality.—R.J.R.

Wilson Bull., 94(3), 1982, pp. 393–429

LIST OF BOOKS IN THE JOSSELYN VAN TYNE MEMORIAL LIBRARY, THE WILSON ORNITHOLOGICAL SOCIETY



The books and monographs in the Library are catalogued and shelved by the University of Michigan Library and are housed in the Museum of Zoology Bird Division's library room. Except for a few rare items which are non-circulating, the books (like serials, reprints, and records) are mailed out on request to members of the Society in the U.S. and Canada. The University pays postage one way and the borrower pays the return. Members should send inquiries to the Library. When a book is needed, please send a complete citation and any special notes, such as particular editions required.

These volumes have been donated by members, received on exchange, or purchased by the Library. Any donations, especially of books not on the list, or contributions to the new book fund will be gratefully received and acknowledged.

Following is a list of the books, monographs, and separately catalogued items currently in the Josselyn Van Tyne Memorial Library. Books are listed alphabetically by author or editor. Multiple editions are indicated by dates. Multiple copies of any edition are not noted. A complete list of books was last published in 1952, and the last supplement in 1965. For a list of currently received serial publications, see Wilson Bulletin 1978, Vol. 90, No. 4, pp. 673–678.

Sincere appreciation goes to Linda Lutz and Betsy Johns for compiling and typing the list.

JANET HINSHAW, *Librarian, Wilson Ornithological Society, Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109. Telephone 313-764-0457.*

Aagaard, C. J. 1930. The common birds of Bangkok.
Abbott, C. C. 1895. The birds about us.
Abbott, C. G. 1911. The home-life of the Osprey.
Acworth, C. G. 1956. Bird and butterfly mysteries—the truth about migration.
Adams, C. C. 1906. An ecological survey in northern Michigan.
———. 1909. An ecological survey of Isle Royale, Lake Superior.
Agassiz, A. 1913. Letters and recollections of Alexander Agassiz.

Agassiz, L., H. E. Strickland, and W. Jardine. 1848–54. Bibliographia zoologiae et geologiae. Vols. 1–4.
Aiken, C. and E. R. Warren. 1914. The birds of El Paso County, Colorado.
Akademiia nauk Kazakhskoi SSR. 1960. PtitsyKazakhatana. [Birds of Kazakhstan.]
Akademiia nauk SSSR. 1966. Mekhanizmy poleta i orientatsii ptits. [Mechanisms of flight and orientation of birds.]
———. 1976. Koltsevanie v izuchenii migratsii ptits fauny SSSR. [Ringing in the study of migratory birds in the USSR.]
Aldrich, J. W. and B. Patterson, Jr. 1937. The birds and mammals of the western slope of the Azuero Peninsula.
Alexander, W. B. 1928. Birds of the ocean.
Ali, S. 1946, 1955, 1961, 1964, 1968. The book of Indian birds.
———. 1949. Indian hill birds.
———. 1962. The birds of Sikkim.
Alicata, J. E. 1964. Parasitic infections of man and animals in Hawaii.
Allee, W. C. 1951. Cooperation among animals.
———, A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. Principles of animal ecology.
Allen, A. A. 1930, 1936. The book of bird life.
———. 1936, 1947. Ornithology laboratory notebook.
———. 1939. The Golden Plover and other birds.
———. 1951. Stalking birds with color camera.
———, L. A. Fuertes, and M. D. Pirnie. 1927. General ornithology laboratory notebook.
Allen, E. G. 1951. The history of American ornithology before Audubon.
Allen, G. M. 1924. An introduction to the study of birds.
———. 1925. Birds and their attributes.
Allen, J. A. 1868. Notes on birds observed in western Iowa in the months of July, August and September.
———. 1916. Autobiographical notes and a bibliography of the scientific publications of Joel Asaph Allen.
Allen, R. P. 1947. The flame birds.
———. 1957. On the trail of vanishing birds.
———. 1961. Birds of the Caribbean.
Allouse, B. E. 1950. A handlist of the birds of Iraq.
———. 1960–62. Birds of Iraq. Vols. 1–3.
Altum, B. 1869. Der Vogel und sein Leben.
Amadon, D. 1966. Birds around the world.
Ambedkar, V. C. 1964. Some Indian weaver birds.
American Ornithologists' Union. 1886. Code and checklist of North American birds.
———. 1889 Abridged, 1895, 1910, 1910 Abridged, 1931, 1935 Abridged, 1957. Check-list of North American birds.
———. 1889. Supplement to the AOU code.
———. 1892, 1908. The code of nomenclature.
———. 1933. Fifty years' progress of American ornithology.
Ames, J. G. 1893. Comprehensive index of the publications of the United States government, 1889–1893.
Ammann, G. A. 1957. The prairie grouse of Michigan.
Anderson, A. H. and A. Anderson. 1973. The Cactus Wren.
Anderson, R. M. 1907. The birds of Iowa.
———. 1949. Methods of collecting and preserving vertebrate animals.

Ap Evans, H. 1960. Falconry for you.
Apgar, A. C. 1898. Birds of the United States east of the Rocky Mountains.
Arbib, R. and T. Soper. 1971. The hungry bird book.
Armstrong, E. A. 1942. Bird display.
———. 1947, 1965. Bird display and behavior.
———. 1949. Bird life.
———. 1955. The wren.
Arthur, S. C. 1931. The birds of Louisiana.
Aschenbrenner, A. H. 1932. Il canarino.
Atkinson-Willes, G. L. 1963. Wildfowl in Great Britain.
Audubon, J. J. 1839. Synopsis of the birds of North America.
———. 1929. Journal of J. J. Audubon . . . , 1820–1821.
———. 1929. Journal of J. J. Audubon . . . , 1840–43.
———. 1937. The birds of America.
———. 1950. Audubon's birds of America.
Audubon, M. R. 1960. Audubon and his journals. Vols. 1, 2.
Austin, O. L., Jr. 1961. Birds of the world.
———. 1968. Antarctic bird studies.
———. 1971. Families of birds.
——— and N. Kuroda. 1953. The birds of Japan.
Austing, G. R. and J. B. Holt, Jr. 1966. The world of the Great Horned Owl.
Aymar, G. C. 1938. Bird flight.
Baerg, W. J. 1931. Birds of Arkansas.
———. 1941. Elementary ornithology.
Bailey, A. M. 1943. The birds of Cape Prince of Wales, Alaska.
———. 1948. Birds of arctic Alaska.
———. 1955. Birds of New Zealand.
——— and R. J. Niedrach. 1965. Birds of Colorado. Vols. 1, 2.
——— and J. H. Sorensen. 1962. Subantarctic Campbell Island.
Bailey, B. H. 1906. Two hundred wild birds of Iowa.
———. 1918. The raptorial birds of Iowa.
Bailey, F. M. 1898. Birds of village and field.
———. 1921, 1927. Handbook of birds of the western United States.
———. 1928. Birds of New Mexico.
———. 1939. Among the birds in the Grand Canyon country.
Bailey, H. H. 1925. The birds of Florida.
Bailey, W. 1955. Birds in Massachusetts: when and where to find them.
Baily, W. L. 1875. Our own birds.
Baird, S. F. 1858. Explorations and surveys for a railroad route from the Mississippi River to the Pacific Ocean. Vol. 9, Birds.
———. 1859. Birds of the boundary.
———. 1860. The birds of North America. Atlas.
———. 1864. Review of American birds in the museum of the Smithsonian Institution.
———. 1870. Ornithology. Vol. 1, Land birds.
———. 1963. Correspondence between Spencer Baird and Louis Agassiz.
———, T. M. Brewer, and R. Ridgway. 1905. History of North American birds. Vols. 1–3.
Baker, E. C. S. 1922. The fauna of British India. Vols. 4, 7.
Baker, J. H. 1941. The Audubon guide to attracting birds.
Baldwin, P. H. and D. E. Oehlerts. 1964. The status of ornithological literature.

Baldwin, S. P. 1915–37. Research and bird banding notes. Vols. 1–43.
——— and S. C. Kendeigh. 1932. Physiology of the temperature of birds.
———, H. C. Oberholser, and L. G. Worley. 1931. Measurements of birds.
Bannerman, D. A. and W. M. Bannerman. 1958. Birds of Cyprus.
Barbour, T. 1923. The birds of Cuba.
———. 1943. Naturalist at large.
———. 1943. Cuban ornithology.
———. 1945. A naturalist in Cuba.
———. 1946. A naturalist's scrapbook.
Barclay-Smith, P. 1946. Garden birds.
Barger, N. R., E. E. Bussewhite, E. L. Loyster, S. Robbins, and W. L. Scott. 1942. Wisconsin birds.
Barnés, V. 1940. Las aves de la península de Paraguaná.
Barrows, W. 1889. The English Sparrow (*Passer domesticus*) in North America, especially in its relations to agriculture.
———. 1912. Michigan bird life.
Barruel, P. 1953. Vie et moeurs des oiseaux.
———. 1954. Birds of the world, their life and habits.
Barton, R. 1955. How to watch birds.
Bartram, J. and W. Bartram. 1957. John and William Bartram's America.
Bastock, M. 1967. Courtship; an ethological study.
Batchelder, C. F. 1951. A bibliography of the published writings of William Brewster.
Bates, G. L. 1930. Handbook of the birds of West Africa.
Bates, H. J. and R. L. Busenbark. 1967. Parrots and related birds.
Bates, M. 1950. The nature of natural history.
Bates, R. S. P. and E. H. N. Lowther. 1952. Breeding birds of Kashmir.
Baumgart, W. 1978. Der Sakerfalke: *Falco cherrug*.
Baynes, E. H. 1915. Wild bird guests.
Beardslee, C. S. and H. D. Mitchell. 1965. Birds of the Niagara frontier region.
Bechstein, J. M. 1856. Cage and chamber-birds.
Becker, B. 1930. Birds and birdhouses.
Beczy, T. 1971. Catalogue of the oological collection of the museum in Oradea.
Beddard, F. 1898. The structure and classification of birds.
Bedford, Duke of. 1954. Parrots and parrot-like birds.
Beebe, F. L. 1974. Field studies of the Falconiformes of British Columbia.
Beebe, C. W. 1905. Two bird lovers in Mexico.
———. 1906. The bird: its form and function.
———. 1918–22. A monograph of the pheasants. Vols. 1–4.
———. 1925. Jungle peace.
———. 1926. The Arcturus adventure.
———. 1927. Pheasant jungles.
———, G. I. Hartley, and P. G. Howes. 1917. Tropical wild life in British Guiana.
Beecher, W. J. 1942. Nesting birds and the vegetation substrate.
Beehler, B. McP. 1978. Birdlife of the Adirondack Park.
Beetham, B. 1910. The home-life of the spoonbill, the stork and some herons.
———. 1911. Photography for bird-lovers.
Behle, W. H. 1958. The bird life of Great Salt Lake.
——— and M. L. Perry. 1975. Utah birds: check-list, seasonal and ecological occurrence charts and guides to bird finding.
Belcher, C. F. 1930. The birds of Nyasaland.

Belding, L. 1890. Land birds of the Pacific district.
Bell, A. 1956. Some common Australian birds.
Bellrose, F. C. 1976. Ducks, geese and swans of North America.
Belopol'skii, L. O. 1957. Ekologiia morskikh kilonial'nykh ptits Barestsova moria. [The ecology of sea colony birds of the Barents Sea.]
Beme, R. L. and A. A. Kuznetsov. 1966. Ptitsy lesov i gor SSSR. [The birds of forests and mountains USSR.]
Bendire, C. 1892–96. Life histories of North American birds. Vols. 1,2.
Bené, F. 1946. The feeding and related behavior of hummingbirds.
Benirschke, K. and T. C. Hsu. (eds.). 1973. Chromosome atlas: fish, amphibians, reptiles and birds. Vol. 2.
Bennett, L. J. 1938. The Blue-winged Teal.
Bennett, R. B. 1962. Care and breeding of budgerigars, canaries and foreign finches.
Benson, C. W. and F. M. Benson. 1977. The birds of Malawi.
——— and C. M. N. White. 1957. Check list of the birds of Northern Rhodesia.
Bent, A. C. 1921, 1947. Life histories of North American gulls and terns.
———. 1922. Life histories of North American petrels and pelicans and their allies.
———. 1923, 1925. Life histories of North American wild fowl. Pts. 1 and 2.
———. 1927, 1929. Life histories of North American shore birds. Pts. 1 and 2.
———. 1932. Life histories of North American gallinaceous birds.
———. 1937, 1938. Life histories of North American birds of prey. Pts. 1 and 2.
———. 1939. Life histories of North American woodpeckers.
———. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds and their allies.
———. 1942. Life histories of North American flycatchers, larks, swallows and their allies.
———. 1946. Life histories of North American jays, crows and titmice.
———. 1946. Life histories of North American diving birds. (reprint)
———. 1948. Life histories of North American nuthatches, wrens, thrashers and their allies.
———. 1949. Life histories of North American thrushes, kinglets and their allies.
———. 1950. Life histories of North American wagtails, shrikes, vireos and their allies.
———. 1953. Life histories of North American wood warblers.
———. 1958. Life histories of North American blackbirds, orioles, tanagers and their allies.
———. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows and their allies. Pts. 1–3.
Berg, B. 1930. To Africa with the migratory birds.
———. 1952. Eyes in the night.
Berger, A. J. 1961. Bird study.
———. 1972. Hawaiian birdlife.
Bergtold, W. H. 1917. A study of the incubation periods of birds.
———. 1928. A guide to Colorado birds.
Berlioz, J. 1941. La vie des oiseaux.
———. 1946. Faune de l'empire Francais. IV. Oiseaux de la Réunion.
———. 1953. Petit atlas des oiseaux. Vols. 1–4.
Bernis Madrazo, F. 1966. Migracion en aves tratado teorico y practico.
———. 1970–71. Aves migradoras ibéricas; según anillamientos en Europa. Vols. 6–8.
Bewick, T. 1947. A selection of engravings on wood by Thomas Bewick.
Bickerton, W. 1912. The home life of the terns or sea swallows.

Blackwelder, R. E. 1967. Taxonomy.
Blagoveschchenskii, D. I. 1959. Fauna USSR. Vol. 1, No. 1, Sect. 1. Bird lice.
Blake, E. R. 1953. Birds of Mexico.
Blanchan, N. 1907. Bird neighbors.
———. 1908. Birds that hunt and are hunted.
———. 1939. The bird book.
Blatchley, W. S. 1898. Indiana. Twenty-second annual rept. Dept. geology and natural resources.
Blyth, E. and W. B. Tegetmeier. 1881. The natural history of the cranes.
Boas, J. E. V. 1929. Biologisch-anatomische studien über den hals der vögel.
Boetticher, H. von. 1952. Banse—und Entenvogel aus aller Welt.
Bolles, F. 1894. From Blomidon to Smoky, and other papers.
Bonaparte, C. L. 1825–28. American ornithology.
———. 1838. A geographical and comparative list of the birds of Europe and North America.
Bond, J. 1936. Birds of the West Indies.
———. 1940, 1945, 1950, 1956. Check-list of birds of the West Indies.
———. 1947. Field guide to birds of the West Indies.
———. 1956–1974. Supplements to the check-list of birds of the West Indies. Nos. 1–19.
Bonhote, J. L. 1907. Birds of Britain.
Boosey, E. J. 1956? Foreign bird keeping.
Booth, E. S. 1948. Birds of the west.
Bosschère, J. de. 1933. Les paons et autres merveilles.
Bouet, G. 1955. Oiseaux de l'afrique tropicale. Pt. 1.
Boyd, A. W. 1946. The country diary of a Cheshire man.
———. 1951. A country parish.
Brand, A. R. 1934. Songs of wild birds.
———. 1936. More songs of wild birds.
Brandt, H. 1940. Texas bird adventures in the Chisos Mountains and on the northern plains.
———. 1943. Alaska bird trails.
———. 1951. Arizona and its bird life.
Bready, M. B. 1929. The European Starling on his westward way.
Brehm, A. E. 1871? Cassell's book of birds. Vol. 3.
Brewster, W. 1886. Bird migration.
———. 1906. Birds of the Cambridge region of Massachusetts.
———. 1924–1938. The birds of the Lake Umbagog region of Maine. Pts. 1–4.
———. 1936. October farm.
———. 1937. Concord River.
Brimley, H. H. 1949. A North Carolina naturalist, H. H. Brimley.
Brimont, R. de. 1932. Les oiseaux.
British Museum. 1891, 1893. Catalogue of the birds in the British Museum. Vols. 19, 21.
———. 1903–40. Catalogue of the books, manuscripts, maps and drawings in the British Museum. Vols. 1–8.
British Ornithologists' Union. 1952. Check-list of the birds of Great Britain and Ireland.
Broley, M. J. 1952. Eagle man.
Bronson, J. L. 1953. Parrot family birds.
Brooks, E. A. 1938. A descriptive bibliography of West Virginia ornithology.
Broun, M. 1949. Hawks aloft: the story of Hawk Mountain.

Brouwer, H. A. (ed.). 1925. Practical hints to scientific travellers. Vol. 3.
Brown, L. 1947. Birds and I.
———. 1955. Eagles.
———. 1976. British birds of prey: a study of Britain's 24 diurnal raptors.
Brown, P. and G. Waterston. 1962. The return of the Osprey.
Brown, R. G. B., D. N. Nettleship, P. Germain, C. E. Tull, and T. Davis. 1975. Atlas of eastern Canadian seabirds.
Brudnell-Bruce, P. G. C. 1975. The birds of New Providence and the Bahama Islands.
Bruner, L., R. H. Wolcott, and M. H. Swenk. 1904? A preliminary review of the birds of Nebraska.
Bruner, P. L. 1972. Field guide to the birds of French Polynesia.
Bruun, B. and A. Singer. 1971. Birds of Europe.
Bryan, W. A. 1901. A key to the birds of the Hawaiian group.
Buchanan, R. 1913. Life of Audubon the naturalist.
Buckley, P. A. and F. G. Buckley. 1978. Guidelines for protection and management of colonially nesting waterbirds.
Bucknill, Sir J. A. S. and F. N. Chasen. 1927. The birds of Singapore Island.
Buechner, H. K. and J. H. Buechner. (eds.). 1970. The avifauna of northern Latin America.
Buick, T. L. 1931. The mystery of the moa.
Bull, J. 1974. Birds of New York State.
———. 1976. Supplement to birds of New York State.
Buller, W. L. 1882. Manual of the Birds of New Zealand.
Bump, G., R. W. Darrow, F. C. Edminster, and W. F. Crissey. 1947. The Ruffed Grouse: life history, propagation, management.
Burghi, J. 1942. Pajaros nuestros.
Burns, F. 1915. A bibliography of scarce or out of print North American amateur and trade periodicals devoted more or less to ornithology.
———. 1919. The ornithology of Chester County, Pennsylvania.
Burton, J. A. (ed.). 1973. Owls of the world.
Burton, P. J. K. 1974. Feeding and the feeding apparatus in waders.
Burtt, H. E. 1967. The psychology of birds.
Buss, I. O. 1946. Wisconsin pheasant populations.
Butler, T. Y. 1979. Birds of Ecuador and the Galapagos archipelago.
Buturlin, S. A. and G. P. Dementiev. 1933–35. Systema avium Rossicarum. Vol. I.
Buxton, J. 1950. The Redstart.
Bykhovskii, B. E. (ed.). 1971. Bird migrations.
Cain, A. J. 1954. Animal species and their evolution.
Caldwell, H. R. and J. C. Caldwell. 1931. South China birds.
Cameron, A. and C. J. O. Harrison. 1978. Bird families of the world.
Campbell, B. 1953. Finding nests.
Campbell, L. W. 1968. Birds of the Toledo area.
Capen, E. A. 1886. Oölogy of New England.
Carpenter, J. R. 1938. An ecological glossary.
Carr, W. H. 1931. Glimpses of familiar birds.
———. 1947. Desert parade.
Carson, R. 1962. Silent spring.
Carus, J. V. and W. Engelmann. 1861. Bibliotheca zoologica. vols. 1, 2.
Catchpole, C. 1979. Vocal communication in birds.
Cătuneanu, I. I., S. Pesqouschi, M. Talpeana, and F. Theiss. 1971. Bibliographia ornithologica Romaniae.

Cayley, N. W. 1935. What bird is that? A guide to the birds of Australia.
———. 1949. The fairy wrens of Australia.
Černý, W. and M. Klíma. 1956. Sborník přednášek. [A collection of lectures.]
Chamberlain, F. W. 1944. Atlas of avian anatomy.
Chance, E. P. 1940. The truth about the cuckoo.
Chapin, J. P. 1932–54. The birds of the Belgian Congo. Vols. 1–4.
Chapman, F. M. 1897, 1900, 1907, 1911, 1912, 1921, 1932. Handbook of birds of eastern North America.
———. 1899, 1919, 1927. Bird-life.
———. 1900. Bird studies with a camera.
———. 1903, 1912. Color key to North American birds.
———. 1907. The warblers of North America.
———. 1908. Camps and cruises of an ornithologist.
———. 1916. The travels of birds.
———. 1918. Our winter birds.
———. 1920, 1929. What bird is that?
———. 1929. My tropical air castle.
———. 1933. Autobiography of a bird lover.
———. 1938. Life in an air castle.
Cherrie, G. K. 1916. A contribution to the ornithology of the Orinoco region.
Christy, B. H. (ed.). 1929. The book of Huron Mountain.
Chubb, C. 1916, 1921. The birds of British Guiana. Vols. 1, 2.
Clancey, P. A. 1953. A preliminary list of the birds of Natal and Zululand.
———. 1964. The birds of Natal and Zululand.
———. 1971. A handlist of the birds of southern Mocambique.
——— et al. 1969. Check list of the birds of South Africa.
Clark, R. J., D. G. Smith, and L. H. Kelso. 1978. Working bibliography of owls of the world: with summaries of current taxonomy and distributional status.
Clarke, F. E. (ed.). 1940. Great wings and small.
Clarke, W. E. 1912. Studies in bird migration. Vols. 1, 2.
Clear, V. 1966. Common cagebirds in America.
Clements, J. F. 1974. Birds of the world: a checklist.
Cohen, E. 1963. Birds of Hampshire and the Isle of Wight.
Colbert, E. H. 1955. Evolution of the vertebrates.
Colorado Field Ornithologists. 1978. Colorado bird distribution latilong study.
Commissie voor de Nederlandse avifauna. 1962. Avifauna van Nederland.
Commons, M. A. 1938. The log of Tanager Hill.
Conference of Biological Editors. 1960. Style manual for biological journals.
Congdon, R. T. 1954. Our beautiful western birds.
Connett, E. V. (ed.). 1930. Upland game bird shooting in America.
Cook, A. J. 1893. Birds of Michigan.
Cooke, W. W. 1888. Report on bird migration in the Mississippi Valley in the years 1884 and 1885.
———. 1897. The birds of Colorado.
———. 1898. Further notes on the birds of Colorado.
Cooper, J. G. 1870. Ornithology, land birds. Vol. 1.
Cory, C. B. 1878. A naturalist in the Magdalen Islands.
———. 1885, 1886. List of the birds of the West Indies.
———. 1899. The birds of eastern North America. Pts. 1, 2.
———. 1909. The birds of Illinois and Wisconsin.

Costello, D. F. 1971. The world of the gull.
Coues, E. 1873. A check list of North American birds.
———. 1874. Birds of the northwest.
———. 1874. Field ornithology.
———. 1878. Birds of the Colorado valley.
———. 1882. The Coues check list of North American birds.
———. 1884, 1890, 1903. Key to North American birds.
Craighead, F. and J. Craighead. 1939. Hawks in the hand.
——— and ———. 1956. Hawks, owls and wildlife.
Cramp, S., W. R. P. Bourne and D. Saunders. 1974. The seabirds of Britain and Ireland.
Crook, J. H. 1964. The evolution of social organization and visual communication in the weaver birds (Ploceinae).
Crosby, M. S. 1916. Rhinebeck birds and seasons.
Cruickshank, A. D. 1942. Birds around New York City.
———. 1947. Wings in the wilderness.
———. 1977. Cruickshank's photographs of birds of America.
———. [?] The birds of Brevard County, Florida.
——— and H. Cruickshank. 1958. 1001 questions answered about birds.
Cruickshank, H. 1948. Flight into sunshine.
———. 1949. Bird islands down east.
Cruz, M. F. and R. Saez-Royuela (eds.). 1971. Homenaje al Prof. Dr. D. Francisco Bernis, en el XV aniversario de la Sociedad Espanola de Ornitologia.
Cuming, E. D. 1913–14. The Bodley Head natural history. Vols. 1, 2.
Curry-Lindahl, K. 1947. Några svenska fåglar. [Some Swedish birds.]
———. 1956. Ecological studies on mammals, birds, reptiles and amphibians in the eastern Belgian Congo. Pt. 1.
Cutright, P. R. 1940. The great naturalists explore South America.
Daglish, E. F. 1932. How to see birds.
Dall, W. H. 1915. Spencer F. Baird: a biography.
Dalrymple, B. W. 1949. Doves and dove shooting.
Danforth, S. T. 1925. Birds of the Cartagena Lagoon, Porto Rico.
———. 1936. Los pájaros de Puerto Rico.
Darling, F. F. 1938. Bird flocks and the breeding cycle.
———. 1943. Wild life of Britain.
Darling, L. and L. Darling. 1962. Bird.
Darlington, P. J., Jr. 1957. Zoogeography: the geographical distribution of animals.
———. 1965. Biogeography of the southern end of the world.
Darwin, C. 1936. The voyage of the Beagle.
D'Aubusson, M. 1928. La protection des oiseaux.
David, Abbé. 1949. Abbé David's diary.
Davie, O. 1898, 1900. Nests and eggs of North American birds.
———. 1900. Methods in the art of taxidermy.
Davis, D. E. 1966. Integral animal behavior.
Davis, D. H. S. (ed.). 1964. Ecological studies in southern Africa.
Davis, L. I. 1972. A field guide to the birds of Mexico and Central America.
Dawson, W. L. 1903. Birds of Ohio.
———. 1923. The birds of California. Vols. 3, 4.
de Beer, G. R. 1937. The development of the vertebrate skull.
———. 1954. Archaeopteryx lithographica.
Deery de Phelps, K. 1953. Aves Venezolanas, cien de las más conocidas.

Deignan, H. G. 1945. The birds of northern Thailand.
———. 1961. Type specimens of birds in the United States National Museum.
———. 1963. Checklist of the birds of Thailand.
Dekay, J. E. 1844. Zoology of New York. Pt. 2. Birds.
Delacour, J. 1947. Birds of Malaysia.
———. 1954–1964. The waterfowl of the world. Vols. 1–4.
——— and D. Amadon. 1973. Curassows and related birds.
——— and P. Jabouille. 1925. Recherches ornithologiques dans la province de Quangtri et quelques autres régions de l'Indochine française.
——— and ———. 1930. Oiseaux des Iles Paracels.
——— and ———. 1931. Les oiseaux de l'Indochine Française. Vols. 1–4.
——— and E. Mayr. 1946. Birds of the Philippines.
Delamain, J. 1928. Pourquoi les oiseaux chantent.
———. 1938. Portraits d'oiseaux.
———. 1948. Les jours et les nuits des oiseaux.
Dementiev, G. P. 1948. Rukovodstvo k opredeleniiu ptits SSSR. [A manual for the delineation of the birds of the USSR.]
———. (ed.). 1955. Materialy po faune iugo-zapadnoi Turkmenii. [Material on the fauna of SW Turkmen.]
——— et al. (ed.). 1970. Birds of the Soviet Union. Vol. 5.
Dennis, J. V. 1975. A complete guide to bird feeding.
de Schauensee, R. M. 1948–52. The birds of the Republic of Colombia. Pts. 1–5.
———. 1964. The birds of Colombia.
———. 1966. The species of birds of South America and their distribution.
———. 1970. A guide to the birds of South America.
——— and W. H. Phelps, Jr. 1978. A guide to the birds of Venezuela.
Dethier, V. G. and E. Stellar. 1961. Animal behavior.
Dewar, D. 1923. Himalayan and Kashmiri birds.
Dewar, J. M. 1924. The bird as a diver.
Dharmakumarshinhji, R. S. 1955. Birds of Saurashtra India.
Dice, L. R. 1943. The biotic provinces of North America.
Dickey, D. R. and A. J. Van Rossem. 1923. The birds of El Salvador.
Dill, H. H. and F. B. Lee (eds.). 1973. Home grown honkers.
Dircksen, R. 1950. Die Insel der Vögel.
———. 1951. Vogelvolk auf weiter Reise.
Dixon, C. 1897. The migration of birds.
———. 1902. Birds' nests.
Dixon, J. S. 1942. Wildlife portfolio of the western national parks.
Dixon, R. 1917. The human side of birds.
Dobzhansky, T. 1941. Genetics and the origin of species.
Dod, A. S. de. 1978. Aves de la República Dominicana.
Dol'nik, V. R. 1975. Migratsionnoe sostoianie ptits. [The migratory status of birds.]
Dorst, J. 1956. Les migrations des oiseaux.
———. 1962, 1963. The migrations of birds.
———. 1974. The life of birds. Vols. 1, 2.
Drost, R. 1930. Über den Vogelzug auf der Schlangeninsel im Schwarzsen Meer.
Douglas, N. 1929. Birds and beasts of the Greek anthology.
Dow, D. (ed.). 1971. Index to current Australian ornithological research.
Dugmore, A. R. 1900. Bird homes.
DuPuy, W. 1938. The nation's forests.

Dwight, J., Jr. 1895. The Ipswich Sparrow (*Ammodramus princeps* Maynard) and its summer home.
———. 1900, 1975. The sequence of plumages and moults of the passerine birds of New York.
Dzubin, A. 1974. Snow and Blue goose distribution in the Mississippi and central flyways.
Eastern Peregrine Falcon Recovery Team. 1976. Eastern Peregrine Falcon recovery plan. Final draft.
Eastman, W. R. and A. C. Hunt. 1966. The parrots of Australia.
Eaton, E. H. 1910, 1914. Birds of New York. Vols. 1, 2.
———. 1916, 1925. Plates reprinted from "Birds of New York."
Eaton, W. P. 1920. In Berkshire fields.
Eckstein, G. 1936. Canary; the history of a family.
Eckstorm, F. H. 1901. The woodpeckers.
Edminster, F. C. 1947. The Ruffed Grouse: its life story, ecology and management.
———. 1954. American game birds.
Edwards, E. P. 1955, 1968. Finding birds in Mexico.
———. 1959. Finding birds in Panama.
———. 1972. A field guide to the birds of Mexico.
———. 1974. A coded list of birds of the world.
———. 1976. 1976 supplement to finding birds in Mexico (1968).
Eesti NSV Teaduste Akadeemia Juures. 1970. Laane-Eesti Rannikualade Loodus. [Nature in the west Estonian coastal areas.]
Eesti NSV Teaduste Akadeemia. 1972. Looduskaitse ja teaduslik uurimistoo. [Nature protection and scientific research.]
Ehrhart-Dachau, O. 1930. Das sterbende Moor.
Eifert, V. S. 1941. Birds in your back yard.
Einarsen, A. S. 1965. Black Brant.
Eisenmann, E. 1955. The species of Middle American birds.
Ekman, S. 1944. Djur I de svenska fjällen. [Wildlife in the swedish mountains.]
Elliot, D. G. 1865. The game birds of the United States.
———. 1897. The gallinaceous game birds of North America.
———. 1898. The wild fowl of the United States and British possessions.
Elliott, H. W. 1882. A monograph of the Seal Islands of Alaska.
Elton, C. S. 1949. Animal ecology.
———. 1957. The ecology of animals.
Engelmann, W. 1846. Bibliotheca historico-naturalis.
Erskine, A. J. 1971. Buffleheads.
Estonian S. S. R. Rahvusvahelise. 1970. Estonian wetlands and their life.
Etkin, W. (ed.). 1964. Social behavior and organization among vertebrates.
Evans, A. H. (ed.). 1903. Turner on birds.
———. 1935. Birds.
Evermann, B. W. and H. W. Clark. 1920. Lake Maxinkuckee. Vols. 1, 2.
Eyton, T. C. 1867–69. Osteologia avium. Vols. 1–3.
Fables, D., Jr. 1955. Annotated list of New Jersey birds.
Fain, A. 1965. A review of the family Epidermoptidae Trouessart parasitic on the skin of birds (Acarina: Sarcoptiformes). Pts. 1, 2.
Fairbairn, W. A. 1952. Some game birds of West Africa.
Falz-Fein, W. 1930. Askania Nova—Das Tierparadies.
Farner, D. 1952. The birds of Crater Lake National Park.
———. (ed.). 1973. Breeding biology of birds.
——— and J. R. King (eds.). 1971–1975. Avian biology. Vols. 1–5.
Farwell, E. D. 1919. Bird observations near Chicago.

Faull, J. H. (ed.). 1913. The natural history of the Toronto region, Ontario, Canada.
Faunal papers on ornithology (misc. authors). 1840–1921. 6 vols. covering various states and regions; New England, N.Y., Montana, Ill., Iowa, Ohio, Wisc., E. Canada, Va., Md., D.C.
Faxon, W. 1911. Brewster's Warbler.
——— and R. Hoffmann. 1900. The birds of Berkshire County, Massachusetts.
Federal Writers' Project. 1938. Birds of the world.
Feduccia, J. A. 1980. The age of birds.
Fehringer, O. 1922. Die Vögel Mitteleuropas. Vol. I, Singvögel, only.
———. 1951. Die Welt der Vögel.
———. 1961. Der Kuckuck aus dem Leben eines Schmarotzers.
Ferensa, B. 1967, 1971. Klucze do ozanczania kregowcow Polski. Vols. 4A, 4B. Ptaki. [Keys for the designation of the vertebrates of Poland Birds.]
Ferguson-Lees, J. et al. (eds.). 1975. Guide to bird-watching in Europe.
Ferianc, O. 1964–5. Stavovce Slovenska. Vols. 1, 2. [Vertebrates of Slovakia.]
Ferns, P. N. (ed.). 1977. The birds of Gwent.
Feyerabend, C. 1954. The budgerigar as a pet.
ffrench, Richard. 1973. A guide to the birds of Trinidad and Tobago.
Figuier, L. 1873. Reptiles and birds.
Finley, W. L. 1907. American birds.
Finn, F. 1908. The world's birds.
———. 1922. Bird behaviour.
Fisher, A. K. 1893. The hawks and owls of the United States in their relation to agriculture.
Fisher, G. C. (ed.). 1936. Nature's secrets.
Fisher, H. I. 1946. Adaptations and comparative anatomy of the locomotor apparatus of new world vultures.
——— and M. L. Fisher. 1974. Wonders of the world of the albatross.
——— and D. C. Goodman. 1955. The myology of the Whooping Crane, *Grus americana*.
Fisher, J. 1947, 1951, 1955. Bird recognition. Vols. 1–3.
———. 1947. The birds of Britain.
———. 1953. Watching birds.
———. 1954. A history of birds.
———. 1954. Birds as animals.
——— and R. M. Lockley. 1954. Sea-birds.
Fitter, R. S. R. 1953. The pocket guide to British birds.
Fjeldså, J. 1977. Guide to the young of European precocial birds.
Fleming, C. A. et al. (eds.). 1953. Checklist of New Zealand birds.
Flint, V. E., P. L. Bome, U. V. Kostin and A. A. Kuznesov. 1968. Ptitsy SSSR. [Birds of USSR.]
Forbush, E. H. 1907. Useful birds and their protection.
———. 1912. A history of the game birds, wild fowl and shore birds of Massachusetts and adjacent states.
———. 1925, 1927, 1929. Birds of Massachusetts and other New England states. Vols. 1–3.
——— and J. B. May. 1939. Natural history of the birds of eastern and central North America.
Ford, A. (ed.). 1957. The bird biographies of John James Audubon.
Forest & Bird Protection Society of New Zealand. 1948. New Zealand birds.
Formozov, A. N. 1976. Zveri, ptitsy i ikh vzaimosviazi so sredoi obitaniia. [Beasts, birds and their interrelationships in the environment.]
Forshaw, J. M. 1969. Australian parrots.

Fowler, W. W. 1888. Tales of the birds.
Franke, H. 1933. Vogelruf und Vogelsang.
———. 1938. Z-i-i-h—die Beutelmeise.
Fredrich II, Emperor of Germany, 1194–1250. 1943. The art of falconry. Translated by C. A. Wood and F. M. Fyfe.
Freeman, G. E. 1869. Practical falconry.
Frey, E. S. 1943. Centennial check-list of the birds of Cumberland Co., Pennsylvania, and her borders.
Frick, G. F. and R. P. Sterns. 1961. Mark Catesby: the colonial Audubon.
Friedmann, H. 1929. The cowbirds.
———. 1930, 1937. Birds collected by the Childs Frick expedition to Ethiopia and Kenya colony. Pts. 1, 2.
———. 1946. The symbolic goldfinch.
———. 1955. The honey-guides.
———. 1960. The parasitic weaverbirds.
———, L. Griscom and R. T. Moore. 1950, 1957. Distributional check-list of the birds of Mexico. Pts. 1, 2.
Frieling, H. 1940. Liebes- und Brutleben der Vögel.
———. 1950. Was fliegt denn da?
Frith, H. J. 1962. The Mallee-fowl, the bird that builds an incubator.
———. 1967. Waterfowl in Australia.
———. (ed.). 1969. Birds in the Australian high country.
Fuertes, L. A. 1930. Abyssinian birds and mammals.
———. 1932. Portraits of New England birds.
———. 1979. To a young bird artist: letters from Louis Agassiz Fuertes to George Miksch Sutton.
———. See also Marcham, F. G.
——— and W. H. Osgood. 1936. Artist and naturalist in Ethiopia.
Fuller, G. N. (ed.). 1928. Geological reports of Douglass Houghton.
Gabrielson, I. N. and S. G. Jewett. 1940. Birds of Oregon.
Gadow, H. F. 1891. Dr. H. G. Bronn's Klassen und Ordnungen des Thier-Reichs, wissenschaftlich dargestellt in Wort und Bild. Vogel. I. Anatomischer Theil.
———. 1898. A classification of vertebrata, recent and extinct.
Gallatin, F. 1908. Catalogue of a collection of books on ornithology in the library of Frederic Gallatin, Jr.
Gallet, E. 1950. The flamingos of the Camargue.
Garrido, O. H. and F. G. Montaña. 1975. Catálogo de las aves de Cuba.
Gauthreaux, S. A. (ed.). 1974. A conference on the biological aspects of the bird/aircraft collision problems.
Gaze, R. 1943. Look at this bird.
Gee, N. G., L. I. Moffett and G. D. Wilder. 1926–27. A tentative list of Chinese birds. Pts. 1–3.
Geiser, S. W. 1937. Naturalists of the frontier.
Gentry, T. G. 1876. Life-histories of the birds of eastern Pennsylvania. Vol. 1.
Géroudet, P. 1946–57. La vie des oiseaux. Vols. 1–6.
Gibson Hill, C. A. 1949. An annotated checklist of the birds of Malaya.
Giebel, C. G. 1872–7. Thesaurus ornithologiae. Vols. 1–3.
Gill, E. L. 1950. A first guide to South African birds.
Gilliard, E. T. 1950. Notes on a collection of birds from Bataan, Luzon.
———. 1958. Living birds of the world.

Gleason, H. A. 1952. New Britton and Brown illustrated flora. Vols. 1–3.
Glenister, A. G. 1951. The birds of the Malay Peninsula, Singapore and Penang.
Glenister, T. W. 1954. The Emperor Penguin, *Aptenodytes forsteri* Gray. II. Embryology.
Goddard, H. 1928. W. H. Hudson: bird-man.
Godfrey, W. E. 1966. The birds of Canada.
Goethe, C. M. 1955. Garden philosopher.
Goethe, F. 1939. Die Vogelinsel Mellum; Beiträge zur Monographie eines deutschen Seevogelschutzgebietes.
———. 1948. Vogelwelt und Vogelleben im Teutoburgerwald-Gebiet.
Goodall, J. D., A. W. Johnson and R. A. Philippi. 1946, 1951. Las Aves de Chile; su conocimiento y sus costumbres. Vols. 1, 2.
———, ———, and ———. 1957–64. Suplemento de las aves de Chile. Pts. 1, 2.
Good, G. B. (ed.). 1896. The published writings of Philip Lutely Sclater, 1844–1896.
Goodman, D. C. and H. I. Fisher. 1962. Functional anatomy of the feeding apparatus in waterfowl.
Goodrich, A. L. 1946. Birds in Kansas.
Goodrich, E. S. 1930. Structure and development of vertebrates.
Goodwin, D. 1970. Pigeons and doves of the world.
Gordon, S. P. 1943. Wild birds in Britain.
Gore, M. E. J. 1971. The birds of Korea.
——— and A. R. M. Gepp. 1978. Las aves del Uruguay.
Goss, N. S. 1886. Birds of Kansas.
Gotz, G. and A. Kosch. 1938. Quel est donc cet oiseau?
Gould, J. 1861. Introduction to the Trochilidae.
———. 1948. Tropical birds from plates by John Gould.
Graham, F., Jr. 1975. Gulls, a social history.
Grange, W. B. 1948. Wisconsin grouse problems.
Grant, J. B. 1894. Our common birds and how to know them.
Grassé, P.-P. 1950. Traité de zoologie.
Graustein, J. E. 1967. Thomas Nuttall: naturalist; explorations in America.
Grave, B. H. and E. P. Walker. 1916. Wyoming birds and their value to agriculture.
Gray, A. P. 1958. Bird hybrids, a check-list with bibliography.
Great Britain Board of Agriculture and Fisheries. 1912. The grouse in health and in disease.
Green, J. C. and R. B. Janssen. 1975. Minnesota birds: where, when, and how many.
Green, R. 1947. Wing-tips; the identification of birds in flight.
———. 1951. How I draw birds.
Greene, E. R. 1966. A lifetime with the birds: an ornithological logbook.
———, W. W. Griffin, E. P. Odum, H. L. Stoddart, I. R. Tomkins, and E. E. Murphy. 1945. Birds of Georgia.
Greene, W. T. 1883–87. Parrots in captivity. Vols. 1–3.
Greenewalt, C. H. 1960. Hummingbirds.
———. 1975. The flight of birds.
Greenway, J. C., Jr. 1958. Extinct and vanishing birds of the world.
Grieve, S. 1885. The Great Auk, or Gatefowl (*Alca impennis* Linn.).
Grinnell, J. 1943. Joseph Grinnell's philosophy of nature.
———, H. C. Bryant, and T. I. Storer. 1918. The game birds of California.
——— and J. M. Linsdale. 1936. Vertebrate animals of Point Lobos Reserve, 1934–35.
——— and T. I. Storer. 1924. Animal life in the Yosemite.
Griscom, L. 1923. Birds of the New York City region.
———. 1937. A monographic study of the red crossbill.

———. 1947. Modern bird study.
———. 1949. The birds of Concord.
——— and D. E. Snyder. 1955. The birds of Massachusetts, an annotated and revised checklist.
——— and A. Sprunt, Jr. 1957, 1979. The warblers of America.
Groser, H. G. 1911. The book of birds.
Grosjean, J. 1976. Le hibou grand-duc.
Gross, A. O. 1928. The Heath Hen.
Grossman, M. L. and J. Hamlet. 1964. Birds of prey of the world.
Grosvenor, G. and A. Wetmore (eds.). 1937. The book of birds. Vols. 1, 2.
Gruenberg, B. C. 1935. The story of evolution.
Gruson, E. S. 1972. Words for birds.
Grzimek, B. 1972. Grzimek's animal life encyclopedia. Vol. 8, Birds II.
Guide to the vertebrate fauna of the eastern Cape Province, Pts. I, II. 1931–37. Albany Museum, Grahamstown, South Africa.
Gunn, W. W. H. et al. See LGL Ltd.
Gurney, J. H. 1884. A list of the diurnal birds of prey.
———. 1894. Catalogue of the birds of prey.
———. 1913. The Gannet.
———. 1921. Early annals of ornithology.
Gustafson, A. F., H. Ries, C. H. Guise, and W. J. Hamilton, Jr. 1939. Conservation in the United States.
Gyldenstolpe, N. 1916. Zoological results of the Swedish zoological expeditions to Siam. 1911–1912 and 1914–1915. IV. Birds II.
———. 1945. A contribution to the ornithology of northern Bolivia.
———. 1945. The bird fauna of Rio Jurua in western Brazil.
von Haartman, L. 1962. The forehead's lyre.
Haberman, H. et al. 1970. Lääne-Eesti rannikualade loodus. [Forest and coastal wildlife of Estonia.]
Hachisuka, M. 1931. The birds of the Philippine Islands, with notes on the mammal fauna. Pt. 1.
———. 1929, 1930. Contributions to the birds of the Philippines. Nos. 1, 2.
———. 1939. Contributions to the birds of Hainan.
——— and T. Udagawa. 1950. Contributions to the ornithology of Formosa.
Hafez, E. S. E. (ed.). 1962. The behaviour of domestic animals.
Hagberg, K. 1953. Carl Linnaeus.
Hagen, W. 1938. Erp, die Geschichte einer Wildente.
Hagerup, A. T. 1891. The birds of Greenland.
Hahn, P. 1963. Where is that vanished bird?
Hájek, V. 1978. Určování stáří a pohlaví pěvců. [Age and sex determination of song birds.]
Haldane, J. S. 1931. The philosophical basis of biology.
Hall, B. P. (ed.). 1974. Birds of the Harold Hall Australian expeditions.
Hall, H. 1946. The Ruffed Grouse.
———. 1960. A gathering of shore birds.
Halle, L. J. 1947. Spring in Washington.
Hamerstrom, F. 1980. Strictly for the chickens.
Hammer-Purgstall, J., von. 1840. Falknerklee, bestehend in drey ungedruckten Werken über die Falknerey.
Hancock, J. and H. Elliott. 1978. The herons of the world.
Hann, H. W. 1953. The biology of birds.

Hanson, H. C. 1965. The Giant Canada Goose.
——— and R. L. Jones. 1976. The biogeochemistry of Blue, Snow, and Ross' geese.
——— and C. W. Kossack. 1963. The Mourning Dove in Illinois.
Hare, C. E. 1952. Bird lore.
Harman, Ian. 1955. Finches.
Harris, A. B. 1880. How we went birds'-nesting.
Harris, H. 1919. Birds of the Kansas City region.
———. 1928. Robert Ridgeway, with a bibliography of his published writings.
Harris, M. P. 1974. A field guide to the birds of Galapagos.
Harrison, C. 1975. A field guide to the nests, eggs and nestlings of European birds with North Africa and the Middle East.
———. 1978. A field guide to the nests, eggs and nestlings of North American birds.
Harrison, H. H. 1948. American birds in color: land birds.
———. 1979. Field guide to western birds' nests.
Harrison, P. P. O. 1962. Sea birds of the South Pacific Ocean.
Harting, J. E. 1871. The ornithology of Shakespeare. Critically examined, explained and illustrated.
———. 1891. Bibliotheca accipitraria.
Hartshorne, C. 1973. Born to sing.
Harvard African Expedition. 1926–27. The African Republic of Liberia and the Belgian Congo. Vols. 1, 2.
Harvey, E. B., H. E. Kaiser, and L. E. Rosenberg. 1968. Atlas of the domestic turkey (*Meleagris gallopavo*): osteology and myology.
Hatch, P. L. 1892. Notes on the birds of Minnesota.
Hatt, R. T. et al. (eds.). 1948. Island life: a study of the land vertebrates of the islands of eastern Lake Michigan.
Hausman, L. A. 1944. The illustrated encyclopedia of American birds.
———. 1946. Field book of eastern birds.
———. 1948. Birds of prey of northeastern North America.
———. 1951. Beginner's guide to attracting birds.
Haverschmidt, Fr. 1942. Faunistisch Overzicht van de Nederlandsche Broedvogels.
———. 1949. The life of the White Stork.
———. 1963. The Black-tailed Godwit.
———. 1978. Trauerseeschwalbe (*Childonias niger*).
Hay, J. 1974. Spirit of survival; a natural and personal history of terns.
Hayward, C. L. et al. (eds.). 1976. Birds of Utah.
Headley, F. W. 1895. The structure and life of birds.
———. 1912. The flight of birds.
Headstrom, R. 1949. Birds' nests.
———. 1951. Birds' nests of the west.
Heilmann, G. 1927. The origin of birds.
Heintzelman, D. S. 1975. Autumn hawk flights: migrations in eastern North America.
———. 1976. A guide to eastern hawk watching.
———. 1979. A guide to hawk watching in North America.
Hendy, E. W. 1950. More about birds.
Henry, G. M. 1955. A guide to the birds of Ceylon.
Henshaw, H. W. 1902. Birds of the Hawaiian Islands.
———. 1913. Fifty common birds of farm and orchard.
———. 1914. Birds of town and country.
Herklots, G. A. C. 1961. The birds of Trinidad and Tobago.

Herman, C. M. et al. 1976. Bibliography of the avian blood-inhabiting protozoa.
Herrick, F. H. 1901. The home life of wild birds.
———. 1917. Audubon the naturalist. Vols. 1, 2.
———. 1934. The American eagle.
———. 1935. Wild birds at home.
Hess, G. 1951. The bird: its life and structure.
Hesse, R., W. C. Allee, and K. P. Schmidt. 1937. Ecological animal geography.
Hester, F. E. 1973. The world of the Wood Duck.
Hewitt, C. G. 1921. The conservation of the wild life of Canada.
Hewitt, O. H. 1976. Fieldbook of birds of the Florida suncoast.
Hewitt, R. 1940. Bird malaria.
Hibbert-Ware, A. 1938. Report of the Little Owl food inquiry.
Hickey, J. J. 1943. A guide to bird watching.
Hiesemann, M. 1912. How to attract and protect wild birds.
Hillstead, A. F. C. 1945. The Blackbird.
Hindwood, K. A. 1940. The birds of Lord Howe Island.
———. 1966. Australian birds in colour.
Hiraldo, F. et al. 1979. El Quebrantahuesos (*Gypaetus barbatus*).
Hitchcock, A. S. 1951. Manual of the grasses of the United States.
Hochbaum, H. A. 1944. The Canvasback on a prairie marsh.
Hoffmann, Bernh. 1908. Kunst und Vogelgesang in ihren wechselseitigen Beziehungen vom naturwissenschaftlich musikalischen Stand punkte beleuchtet.
Hoffman, R. 1923. A guide to the birds.
———. 1927. Birds of the Pacific States.
Hollom, P. A. D. (ed.). 1952. The popular handbook of British birds.
Holmer, M. R. N. 1926. Bird study in India.
Holton, V. 1939. The Beeps.
Hornaday, W. T. 1892. Taxidermy and zoological collecting.
———. 1914. The American natural history. Vols. 2, 3.
———. 1931. Thirty years war for wild life.
Hortling, I. 1946. Lintukirja: Kuvallinen Retkeilykäsikirja Suomen Linnuista. [Book of birds; an illustrated field guide to the birds of Finland.]
Hosking, E. J. and C. W. Newberry. 1946. More birds of the day.
——— and ———. 1949. Birds in action.
Housse, P. R. 1945. Las aves de Chile.
Howard, E. 1940. A waterhen's worlds.
———. 1920. Territory in bird life.
———. 1929. An introduction to the study of bird behavior.
Howard, L. 1953. Birds as individuals.
Howe, R. H., Jr. 1896. Every bird.
——— and G. M. Allen. 1901. The birds of Massachusetts.
——— and E. Sturtevant. 1899. The birds of Rhode Island.
Howell, A. H. 1924, 1928. Birds of Alabama.
———. 1932. Florida bird life.
Howells, V. 1957. A naturalist in Palestine.
Hoyt, S. F. 1958. In memoriam: J. Southgate Y. Hoyt.
Hubbard, J. P. 1970. Check-list of the birds of New Mexico.
Hudson, G. H. 1953. El naturalista en el Plata.
Hudson, W. H. 1917. Idle days in Patagonia.
———. 1920. Birds in town and village.

———. 1920. Birds of La Plata. Vols. 1, 2.
———. 1923. A hind in Richmond Park.
———. 1923. Rare, vanishing and lost British birds.
Hume, E. E. 1942. Ornithologists of the United States Army Medical Corps.
Humphrey, P. S. (ed.). 1970. Birds of Isla Grande.
Hutson, H. W. P. (ed.). 1956. The ornithologists' guide.
Huxley, J. 1942. Evolution: the modern synthesis.
———. 1949. Bird watching and bird behaviour.
Hvass, H. 1963. Birds of the world.
Hyde, A. S. 1979. Birds of Colorado's Gunnison country.
Il'ichev, V. D. 1975. Lokatsiia ptits. [Bird orientation; adaptive mechanisms of the passive orientation of owls.]
——— and E. K. Vilks. 1978. Prostranstvennaya orientatsiya ptits. [Spatial orientation in birds.]
Il'enko, A. I. 1976. Ekologiia domovykh vorob'ev i ikh ektoparazitov. [Ecology of domestic sparrows and their ectoparasites.]
Imhof, T. A. 1962, 1976. Alabama birds.
Ingersoll, E. (ed.). 1914. Alaskan bird-life.
International Commission on Zoological Nomenclature. 1961. International code of zoological nomenclature adopted by the XV International Congress of Zoology.
Ishizawa, J. T. 1950. Genshoku yachô gaido. [A guide-book of the Japanese birds in life colors.] Vols. 1, 2.
Ishizawa, T. and K. Shimamura. 1933. Tori no su tamago. [Birds' nests and eggs.]
Ivanov, A. I. 1976. Katalog ptits SSSR. [Catalogue of the birds of the USSR.]
Jack, A. 1953. Feathered wings.
James, R. D., P. L. McLaren, and J. C. Barlow. 1976. Annotated checklist of the birds of Ontario.
Jameson, E. W., Jr. 1962. The hawking of Japan.
Jameson, W. 1959. The wandering albatross.
Jaques, F. P. 1942. Birds across the sky.
Jaques, H. E. 1947. How to know the land birds.
——— and R. Ollivier. 1960. How to know the water birds.
Jardine, W. 1833–36. Hummingbirds. The naturalist's library. Ornithology. Vols. 1, 2.
Jefferies, R. 1879, 1889. Wild life in a southern county.
Job, H. K. 1903. Among the waterfowl.
———. 1911. The sport of bird study.
———. 1922. How to study birds.
Johnsen, P. 1953. Birds and mammals of Peary Land in North Greenland.
Johnsgard, P. A. 1965. Handbook of waterfowl behavior.
———. 1973. Grouse and quails of North America.
———. 1974. Song of the north wind.
———. 1978. Ducks, geese, and swans of the world.
Johnson, A. W. 1965, 1967. The birds of Chile and adjacent regions of Argentina, Bolivia, and Peru. Vols. 1, 2.
Johnson, C. E. (compiler). 1970. Contemporary readings in behavior.
Johnson, G. 1926. Nature's program.
Johnson, S. R., W. J. Adams, and M. R. Morrell. 1975. The birds of the Beaufort Sea. Pts. 1, 2.
Johnston, I. H. 1923. Birds of West Virginia.
Jones, L. 1903. The birds of Ohio.

Jørgensen, H. I. 1958. Nomina avium Europaearum.
——— and C. I. Blackburne. 1941. Glossarium Europae avium.
Jouard, H. 1936. Révision systématique des formes Eurasiatiques et spécialement alpestres de *Parus atricapillus*, avec un aperçu de ses formes "chinoises," "japonaises" et américaines.
Joy, N. 1942. How to know British birds.
Judd, S. D. 1902. Birds of a Maryland farm.
Jurek, R. M. 1973. California shorebird study.
Just, T. (ed.). 1939. Conference on plant and animal communities.
Kaftanovskii, Yu. M. 1951. Chistikovye ptitsii Vostochnoy Atlantik. [Alcids of the eastern Atlantic.]
Kale, H. W. (ed.). 1978. Rare and endangered biota of Florida. Vol. II, Birds.
Kalela, O. 1938. Über die Regionale Verteilung der Brutvogel fauna im Flussgebiet des Kokemäenjoki.
Kaletskaya, M. L. (ed.). 1973. Prirodnye resursy Mologo-Sheksniskoi niziny nazemnye posvonochnye. [Natural resources of the Mologo-Sheksnin lowlands terrestrial vertebrates.]
Keast, A., R. L. Crocker, and C. S. Christian. (eds.). 1959. Biogeography and ecology in Australia.
Keeler, C. A. 1893. Evolution of the colors of North American land birds.
———. 1899. Bird notes afield: a series of essays on the birds of California.
Keith, L. B. 1963. Wildlife's ten-year cycle.
Kelker, G. H. 1958. Research methods for the beginner.
Kelso, L. and E. H. Kelso. 1934. A key to the species of American owls, with a list of the owls of the Americas.
——— and ———. 1935. Supplement to a key to species of American owls.
Kemsies, E. 1948. Birds of Cincinnati and southwestern Ohio.
——— and W. Randle. 1953. Birds of southwestern Ohio.
Kendeigh, S. C. 1952. Parental care and its evolution in birds.
Kennard, F. H. 1914. Encouraging birds around the home.
Kepler, A. K. 1977. Comparative study of Todies.
Keyser, L. S. 1901. Babby Redstart and other bird stories.
———. 1902. Birds of the Rockies.
Kieran, J. 1947. Footnotes on nature.
———. 1959. A natural history of New York City.
King, B. F. and E. C. Dickinson. 1975. A field guide to the birds of South-east Asia covering Burma, Malaya, Thailand, Cambodia, Vietnam, Laos, and Hong Kong.
King, W. B. 1981. Endangered birds of the world, the ICBP bird red data book.
Kirkman, F. B. 1937. Bird behaviour.
Kiyosu, Y. 1966. Yachō no jiten. [Ecological book of Japanese birds.]
Klincksieck, P. and T. Valette. 1908. Code des couleurs à l'usage des naturalistes, artistes, commerçants et industriels.
Klopfer, P. H. and J. P. Hailman. 1967. An introduction to animal behavior.
Klůz, Z. 1977. Naše ptactvo v lidovém názvosloví a vědecké terminologii. [Our birds in popular names and scientific terminology.]
Knaak, K. 1938. Ti-it.
Knight, O. W. 1897. A list of the birds of Maine.
———. 1908. The birds of Maine.
Knowlton, F. H. and R. Ridgway. 1909. Birds of the world.
Kobayashi, L. 1956, 1961. Niton no chōrui zukan. [Birds of Japan in natural colours.]

———. 1957. Yachō no sekai. [The world of wild birds.]
Koningsberger, J. C. 1909. De vogels van Java.
Kopman, H. H. 1946. Wild acres: a book of the Gulf coast country.
Kortright, F. H. 1942. The ducks, geese and swans of North America.
Krechmar, A. V. et al. 1978. Ekologiia i rasprostranenie ptits na Severo-Vostoke SSSR. [Ecology and distribution of birds in the north east USSR.]
Krider, J. 1879. Forty years notes of a field ornithologist.
Kumari, E. 1966. Ornithological researches in Estonia.
——— (ed.). 1970. Birds on either side of the Gulf of Finland: proceedings of the 3rd Estonian and Finnish ornithologists' days.
———. 1976. Migratsii ptits. [Bird migration.]
Kumlien, L. and N. Hollister. 1903, 1951. The birds of Wisconsin.
Kuroda, N. 1954. On the classification and phylogeny of the order Tubinares, particularly the shearwaters.
Labuschagne, R. J. 1958–65. Birds of the Kruger and other national parks. Vols. 1–4.
Lack, D. 1945. The Galapagos finches.
———. 1947. Darwin's finches.
———. 1954. The natural regulation of animal numbers.
———. 1966. Population studies of birds.
———. 1968. Ecological adaptations for breeding in birds.
———. 1974. Evolution illustrated by waterfowl.
———. 1976. Island biology.
Lambert, T. 1976. Lambert's birds of garden and woodland.
Lambrecht, K. 1933. Handbuch der palaeornithologie. Vols. 1, 2.
Lancaster, F. M. 1963. The inheritance of plumage colour in the common duck.
Lane, S. G. (ed.). 1974. Bird in the hand.
Lange, D. 1906. How to know the wild birds of Iowa and Nebraska.
Langille, J. H. 1884. Our birds in their haunts.
Lanning, G. 1911. Wild life in China.
Lansdowne, J. F. 1976. Birds of the west coast. Vol. 1.
——— and J. A. Livingston. 1970. Birds of the eastern forest: 2.
Lanyon, W. E. and W. N. Tavolga (eds.). 1960. Animal sounds and communication.
La Touche, J. D. 1925–34. A handbook of the birds of eastern China. Vols. 1, 2.
Laubmann, A. 1939–40. Die Vögel von Paraguay. Vols. 1, 2.
Layton, R. B. 1969. The Purple Martin.
Leach, J. A. 1939. An Australian bird book.
Leberman, R. C. 1976. The birds of the Ligonier Valley.
Legendre, M. 1932. Monographie des mésanges d'Europe.
Lehtonen, I. 1945. Lintuparatiisi Pääkapungin Liepeillä. [Bird paradise on the outskirts of the capital city; the bay of the old city and its birds.]
Lemmon, R. S. 1952. Our amazing birds; the little known facts about their private lives.
Leopold, A. 1931. Report on a game survey of the north central states.
———. 1949. A Sand County almanac.
Leslie, A. S. and A. E. Shipley. 1912. The grouse in health and in disease.
Levick, G. M. 1915. Natural history of the Adelie Penguin.
Lewis, H. F. 1929. The natural history of the Double-crested Cormorant.
Lewis, J. C. 1973. The world of the Wild Turkey.
L. G. L. Ltd. 1973–74. Arctic gas. Biological Report Series. Vols. 1–42. (Biological reports on the proposed route of the gas pipeline, many on birds, ed. by W. W. H. Gunn.)
———. 1974. Bird populations and movements associated with the proposed site of the new Toronto International Airport. Vols. 1–3.

Ligon, J. S. 1961. New Mexico birds and where to find them.
Lincer, J. L. et al. 1978. Working bibliography of the Bald Eagle.
Linduska, J. P. (ed.). 1964. Waterfowl tomorrow.
Linsdale, J. M. 1937. The natural history of magpies.
Lister, R. 1979. The birds and birders of Beaverhills Lake.
Littlejohns, R. T. 1933. The magic voice.
Ljunggren, L. 1969. Studies on seasonal activity in pigeons with aspects on the role of biogenic monoamines in the endocrine organs.
Lockley, R. M. 1936. Birds of the green belt.
———. 1938. I know an island.
———. 1942. Shearwaters.
———. 1948. The cinnamon bird.
———. 1953. Puffins.
Loeser, J. A. 1940. Animal behavior.
Longstreet, R. J. 1930. Bird study in Florida.
Lonnberg, E. 1911. Birds collected by the Swedish zoological expedition to British East Africa.
Løppenthin, B. 1946. Fortegnelse over Danmarks fugle. [Catalogue of the birds of Denmark.]
———. 1967. Danske ynglefugle i fortid og nutid. [Danish breeding birds in the past and present.]
Lorenz, K. 1979. The year of the Greylag Goose.
Low, G. C. 1931. The literature of the Charadriiformes 1894–1928.
Lowe, F. A. 1954. The heron.
Lowery, G. H. 1955, 1960, 1974. Louisiana birds.
Lowther, E. H. N. 1949. A bird photographer in India.
Lucas, A. M. and C. Jamroz. 1961. Atlas of avian hematology.
——— and P. R. Stettenheim. 1972. Avian anatomy: integument.
Luke, L. P. and A. Silver. 1952. Aviaries, bird-rooms and cages.
McAtee, W. L. 1905. The Horned Larks and their relation to agriculture.
———. (ed.). 1945. The Ring-necked Pheasant and its management in North America.
McClure, H. E. 1972. Birds banded in Asia during the MAPS program.
———. 1974. Migration and survival of the birds of Asia.
———, N. Raranaworabhan et al. 1972. Some ectoparasites of the birds of Asia.
McClure, H. E. et al. 1978. Haematozoa in the birds of Eastern and Southern Africa.
McCook, H. C. 1902. Tenants of an old farm.
McCoy, J. J. 1966. The hunt for the Whooping Cranes.
McDermott, J. F. 1965. Audubon in the west.
McElroy, T. P., Jr. 1950. Handbook of attracting birds.
———. 1960. The new handbook of attracting birds.
McGill, A. R. 1970. Australian warblers.
McGregor, R. C. 1909. A manual of Philippine birds.
———. 1920. Some features of the Phillipine Ornis, with notes on the vegetation in relation to the avifauna.
———. 1920. Index to the genera of birds.
——— and E. Marshall. 1931. Philippine birds, their haunts and habits.
——— and D. C. Worcester. 1906. A hand-list of the birds of the Philippine Islands.
McIlhenny, E. A. 1914. The Wild Turkey and its hunting.
———. 1934. Bird city.
McIlwraith, Thomas. 1894. The birds of Ontario.
McKenny, M. 1939. Birds in the garden and how to attract them.

McKinney, F. 1961. An analysis of the displays of the European Eider *Somateria m. mollissima* (L.) and the Pacific Eider *S. m.* v. *nigra* Bonaparte.
McNicholl, M. K. 1975. Manitoba bird studies.
MacDonald, M. 1947. The birds of Brewery Creek.
MacKay, B. K. 1968. Eighty more land birds to know.
MacLennan, J. M. 1958. Russian-English bird glossary.
MacPherson, H. A., A. J. Sturat-Wortley, and G. Saintsbury. 1895. The grouse.
———, ———, and ———. 1896. The partridge.
MacPherson, H. B. 1911. The home-life of a Golden Eagle.
MacSwiney, Marquis of Mashanaglass. 1972. Six came flying.
Mackword-Praed, C. W. and C. H. B. Grant. 1957–60. Birds of eastern and north eastern Africa. Vols. 1, 2.
——— and ———. 1962–63. Birds of the southern third of Africa. Vols. 1, 2.
——— and ———. 1970. Birds of the west central and western Africa. Vols. 1, 2.
Macleod, R. D. 1954. Key to the names of British birds.
Macoun, J. 1903. Catalogue of Canadian birds. Pt. 2.
——— and J. M. Macoun. 1909. Catalogue of Canadian birds.
Magaud d'Aubusson, L. 1928. La protection des oiseaux.
Mailliard, J. 1930. Handbook of the birds of Golden Gate Park, San Francisco.
Makatsch, W. 1951. Der Vögel und seine Jungen.
———. 1952. Der Vögel und sein Ei.
———. 1953. Der Vögel und sein Nest.
———. 1953. Unser Kuckuck.
———. 1954. Die Vögel der Erde.
Malbrant, R. 1952. Faune du centre Africain français.
——— and A. Maclatchy. 1949. Faune de l'équateur Africain français.
Mann, F. G. 1951. Esquema ecológico de selva, sabana y cordillera en Bolivia.
Manuel, C. G. 1936. Fifty Philippine birds.
Marcham, F. G. (ed.). 1971. Louis Agassiz Fuertes and the singular beauty of birds: paintings, drawings, letters.
Marks, J. and J. Moody. 1910. A holiday with the birds.
Marler, P. and W. J. Hamilton. 1966. Mechanisms of animal behavior.
Marples, B. J. 1953. Fossil penguins from the mid-tertiary of Seymour Island.
——— and A. Marples. 1934. Sea terns or sea swallows.
Marsh, O. C. 1880. Odontornithes: a monograph of the extinct toothed birds of North America.
Marshall, A. J. (ed.). 1960. Biology and comparative physiology of birds. Vols. 1, 2.
Martin, A. C. and F. M. Uhler. 1939. Food of game ducks in the United States and Canada.
Mathews, G. M. 1925. The birds of Australia bibliography.
———. 1927. Systema avium Australasianarum. Vols. 1, 2.
——— and E. J. Hallstrom. 1943. Notes on the order Procellariiformes.
Matthews, G. V. T. 1955. Bird navigation.
Matthiessen, P. 1973. The wind birds.
Matvejev, S. D. 1950. Rasprostranjenje i život ptica u Srbiji. (Ornithogeographia Serbica.)
May, J. B. 1935. The hawks of North America.
Mayall, K. M. 1957. Some plants suitable for attracting wildlife.
Mayaud, N. 1936. Inventaire des oiseaux de France.
Mayfield, H. 1960. The Kirtland's Warbler.
Mayr, E. 1941. List of New Guinea birds.
———. 1944. Systematics and the origin of species.

———. 1944. The birds of Timor and Sumba.
———. 1945. Birds of the southwest Pacific.
———. 1963. Animal species and evolution.
———, E. G. Linsley, and R. L. Usinger. 1953. Methods and principles of systematic zoology.
——— and E. Schuz. (eds.). 1949. Ornithologie als biologische Wissenschaft.
Meanley, B. 1975. Birds and marshes of the Chesapeake Bay country.
Meinertzhagen, R. 1959. Pirates and predators.
Meisel, M. 1924. A bibliography of American natural history. The pioneer century, 1769–1865. Vols. 1–3.
Menaboni, A. and S. Menaboni. 1950. Menaboni's birds.
Mendall, H. L. 1958. The Ring-necked Duck in the northeast.
——— and C. M. Aldous. 1943. The ecology and management of the American Woodcock.
Merikallio, E. 1946. Über regionale Verbreitung und Anzahl der Landvögel in Süd- und Mittelfinnland, besonders in deren östlichen Teilen, im Lichte von quantitativen Untersuchungen.
Mershon, W. B. 1907. The Passenger Pigeon.
———. 1923. Recollections of my fifty years hunting and fishing.
Meyerriecks, A. J. 1972. Man and birds; evolution and behavior.
Michelet, J. 1869. The bird.
Michell, E. 1959. The art and practice of hawking.
Michigan Historical Commission. 1921. Michigan bibliography. Vols. 1, 2.
Miller, L. E. 1919. In the wilds of South America.
Miller, O. T. 1901. The first book of birds.
———. 1904. With the birds in Maine.
Milne, H. and C. P. Dau. 1976. A bibliography of eiders.
Milne, L. J. and M. Milne. 1962. The senses of animals and men.
Milne-Edwards, H. 1877. Zoologie.
Mitchell, H. D. and R. F. Anderle. 1970. Birds of the Niagara frontier region: supplement.
Mitchell, M. H. 1935. The Passenger Pigeon in Ontario.
———. 1957. Observations on birds of southeastern Brazil.
Mitchell, P. C. 1900. Thomas Henry Huxley.
Mivart, St. George. 1892. Birds: the elements of ornithology.
Monkman, N. 1958. From Queensland to the Great Barrier Reef.
Monro, R. K. 1944. Australian nature stories.
Monson, G. and A. R. Phillips. 1964. A checklist of the birds of Arizona.
More Game Birds in America. 1932. More waterfowl by assisting nature.
Morgan, A. H. 1939. Field book of animals in winter.
Morlion, M. 1971. Vergelijkende studie van de pterylosis in enkele Afrikaanse genera van de Ploceidae: bijdrage tot de morfologie en de systematiek van de Passeriformes. [A comparative study of pterylosis in individual African genera of Ploceidae.] Vols. 1–3.
Mosby, H. S. and C. O. Handley. 1943. The Wild Turkey in Virginia.
Mountfort, G. 1958. Wild paradise.
Moynihan, M. 1979. Geographic variation in social behavior and in adaptations to competition among Andean birds.
Mudie, R. 1854. The feathered tribes of the British Isles.
Mullens, W. H. 1908. A list of books relating to British birds, published before the year 1815.
———. 1909. Some early British ornithologists and their work.
———. 1924. Catalogue of the highly important library of books on British ornithology.

——— and H. K. Swann. 1917. A bibliography of British ornithology.
Munro, G. C. 1944, 1960. Birds of Hawaii.
Murphy, R. C. 1936. Oceanic birds of South America. Vols. 1, 2.
———. 1953. Land birds of America.
Murphy, S. 1978. Martha's Vineyard decoys.
Murray, J. J. 1947. Wild wings.
———. 1957. The birds of Rockbridge County, Virginia.
Murton, R. K. and N. J. Westwood. 1977. Avian breeding cycles.
Musgrove, J. W. and M. R. Musgrove. 1943. Waterfowl in Iowa.
Myers, H. W. 1923. Western birds.
Narosky, T. 1978. Aves Argentinas: guía para el reconocimiento de la avifauna bonaerense. [Field guide to the birds of Buenos Aires province.]
National Geographic Society. 1915. Common birds of town and country.
———. 1937. The book of birds. Vols. 1, 2.
Naumann, J. F. 1957. Lebensdatellungen deutscher Natur forscher.
Nehrkorn, A. 1899, 1910. Katalog der Eiersammlung: nebst Beschreibungen der ausser-europäischen Eier.
———. 1914. Nachträge zur Nehrkorn's Eierkatalog.
Nehrling, H. 1893, 1896. Our native birds of song and beauty. Vols. 1, 2.
Neifel'dt, J. A. (ed.). 1978. Sistematika, morfologiya i biologiya ptits. [Systematics, morphology and the biology of birds.]
Nelson, B. 1978. The Sulidae: gannets and boobies.
Nelson, E. W. 1883. Birds of the Bering Sea and the Arctic Ocean.
———. 1887. Report on the natural history collections made in Alaska between the years 1877 and 1881.
Nelson, T. 1956. The history of ornithology at the University of Michigan Biological Station. 1909–1955.
Nesbit, W. 1926. How to hunt with the camera.
Nethersole-Thompson, D. 1951. The Greenshank.
———. 1973. The Dotterel.
Neuffer, C. H. (ed.). 1960. The Christopher Happoldt Journal.
New Zealand Native Bird Protection Society. The "three castles" book of New Zealand birds.
Newton, A. 1893–96. A dictionary of birds.
Newton, I. 1973. Finches.
Nice, M. M. 1931. The birds of Oklahoma.
———. 1937, 1943. Studies in the life history of the Song Sparrow, I and II.
———. 1939. The watcher at the nest.
Nicholson, E. M. 1931. The art of bird-watching.
——— and L. Koch. 1936. Songs of wild birds.
——— and ———. 1949. More songs of wild birds.
Nicholson, J. C. 1981. The birds of Manitoulin Island.
Nicolai, J. 1974. Bird life.
Nicoll, M. J. 1919. Handlist of the birds of Egypt.
Nihon Chōgakkai. 1922, 1942, 1958. A hand-list of the Japanese birds.
———. 1974. Check-list of Japanese birds.
Nissen, C. 1936. Schöne Vogelbücher, ein Überblick der Ornithologischen Illustration Nebst Bibliographie.
Nitzsch, C. L. 1867. Pterylography.
Noll, H. 1924. Sumpfvogelleben.

———. 1942. Schweizer Vogelleben.
Novaes, F. C. 1973. Aves de una vegetacao secundaria na fox do Amazonas.
Nozeman, C. 1948. Nederlandsche vogelen 1770–1829.
Nuttall, T. 1832. A manual of the ornithology of the United States and of Canada. The land birds.
———. 1834. A manual of the ornithology of the United States and of Canada. The water birds.
Oakes, C. 1953. The birds of Lancashire.
Oberholser, H. C. 1914. A monograph of the genus *Chordeiles* Swainson, type of a new family of goatsuckers.
———. 1917. The birds of the Anamba Islands.
———. 1938. The bird life of Louisiana.
———. 1974. The bird life of Texas. Vols. 1, 2.
Oehser, P. H. (Compiler). 1971. Index to Bent's "Life histories of North American birds."
Officer, H. R. 1971. Australian honeyeaters.
———. 1974. Australian flycatchers and their allies.
Ogilvie, M. A. 1976. Winter birds.
———. 1978. Wild geese.
Oliver, W. R. B. 1930. New Zealand birds.
Olivier, G. 1944. Monographie des Pies-Grièches du genre *Lanius*.
Olrog, C. C. 1959. Las aves Argentinas.
Ornithological Researches in Estonia. 1966. A survey of trends and achievements.
Ortlieb, R. 1979. Die Sperber.
Osborn, H. F. 1924. Impressions of great naturalists.
Over, W. and C. S. Thomas. 1921. Birds of South Dakota.
Palmer, R. S. 1941. A behavior study of the Common Tern (*Sterna hirundo hirundo* L.).
———. 1949. Maine birds.
———. (ed.). 1962, 1976. Handbook of North American birds. Vols. 1–3.
——— et al. 1954. Biographies of members of the American Ornithologists' Union.
Paludan, K. 1947. Alken.
Panov, E. N. 1978. Mekhanizmy kommunikatsii u ptits. [Mechanisms of communication among birds.]
Parham, H. J. 1937. A nature lover in British Columbia.
Parkhurst, H. E. 1894. The birds' calendar.
———. 1901. How to name the birds.
Parker, E. 1935. Ethics of egg-collecting.
Parmelee, A. 1959. All the birds of the Bible.
Parmelee, D. F. 1980. Bird island in Antarctic waters.
Patchett, M. E. 1960. The proud eagles.
Patten, B. M. 1929. The early embryology of the chick.
Patterson, R. L. 1952. The Sage Grouse in Wyoming.
Patton, D. R. and P. F. Ffolliott. 1975. Selected bibliography of wildlife and habitats for the southwest.
Payne, R. S. 1923. The Baltimore Oriole and a biographical sketch of Audubon.
Paynter, R. A. and A. M. G. Caperton. 1977. Ornithological gazeteer of Paraguay.
——— and M. A. Traylor. 1977. Ornithological gazetteer of Ecuador.
———, ———, and B. Winter. 1975. Ornithological gazetteer of Bolivia.
Peabody, S. H. 1868. Cecil's book of birds.
Pearse, T. 1968. Birds of the early explorers in the northern Pacific.
Pearson, R. 1972. The avian brain.

Pearson, T. G. 1917. The bird study book.
———. 1937. Adventures in bird protection.
———, C. S. Brimley, and H. H. Brimley. 1919, 1942, 1959. Birds of North Carolina.
——— et al. (eds.). 1936. Birds of America.
Peattie, D. C. 1935. Singing in the wilderness.
———. 1936. Green laurels.
———. (ed.). 1940. Audubon's America.
Peckover, W. S. 1976. Birds of New Guinea and tropical Australia.
Penny, M. 1974. The birds of Seychelles and the outlying islands.
Percy Fitzpatrick Institute of African Ornithology. 1969[?] Bird-watchers manual of the Percy Fitzpatrick Institute of African Ornithology.
Pereyra, J. A. 1937. Contribucion al estudio y observaciones ornitologicas de la zona norte de la gobernacion de La Pampa.
———. 1943. Nuestras aves.
Perrins, C. 1976. Birds: their life, their ways, their world.
Perry, R. 1946. A naturalist on Lindisfarne.
———. 1948. Shetland sanctuary.
Peters, H. S. and T. D. Burleigh. 1951. The birds of Newfoundland.
Peters, J. L. 1931–1979. Checklist of birds of the world. Vols. 1–10, 12–15.
Peterson, A. M. 1937. The ABC of attracting birds.
Peterson, R. T. 1935. Series of leaflets published by the National Assoc. Audubon Soc.
———. [?] Audubon birds of America.
———. 1934, 1939, 1947, 1980. A field guide to the birds.
———. 1941, 1961. A field guide to western birds.
———. 1948. Birds over America.
———. 1949, 1962. How to know the birds.
———. 1951. Wildlife in color.
———. (ed.). 1957. The bird watcher's anthology.
———. 1960. A field guide to the birds of Texas.
———. 1963. The birds.
——— and E. L. Chalif. 1973. A field guide to Mexican birds.
——— and J. Fisher. 1955. Wild America.
———, G. Mountfort, and P. A. D. Hollom. 1954. A field guide to the birds of Britain and Europe.
Petrak, M. L. (ed.). 1969. Diseases of cage and aviary birds.
Pettingill, O. S., Jr. 1936. The American Woodcock.
———. 1939, 1946, 1956, 1970. A laboratory and field manual of ornithology.
———. 1951, 1977. A guide to bird finding east of the Mississippi.
———. 1953. A guide to bird finding west of the Mississippi.
———. (ed.). 1960. Enjoying Maine birds.
———. (ed.). 1965. The bird watcher's America.
———. 1974. Ornithology at the Universtiy of Michigan Biological Station and the birds of the region.
——— and N. R. Whitney, Jr. 1965. Birds of the Black Hills.
Pfeifer, S. 1950. Taschenbuch der deutschen Vogelwelt.
Phelps, K. D. de. 1954. Aves Venezolanas: cien de las mas conocidas.
Phelps, W. H. 1944. Las aves de Perijá.
Phillips, A. R., J. T. Marshall, and G. Monson. 1964. The birds of Arizona.
Phillips, J. C. 1926. Bibliography of a natural history of the ducks.
———. 1930. American game mammals and birds. A catalogue of books 1582–1925.

——— and F. C. Lincoln. 1930. American waterfowl.
Phillips, W. J. 1963. The book of the Huia.
Phillips, W. W. A. 1953. A revised checklist of the birds of Ceylon.
Pickwell, G. B. 1931. The Prairie Horned Lark.
Pikula, J. 1976. Metodika výzkumu hnízdní bionomie ptactva. [Methodology of research into the breeding biology of birds.]
Pinto, O. M. de O. 1938–44. Catalogo das aves do Brasil. Vols. 1, 2.
———. 1964. Ornitologia Brasiliense.
Pirnie, M. D. 1935. Michigan waterfowl management.
Pitelka, F. A. 1938. Portraits of American birds.
Pitt, F. 1935. Birds and the sea.
Pizzey, G. 1980. A field guide to the birds of Australia.
Polivanov, V. M. 1981. Ekologiya ptits-dyplognezdnikov Primor'ya. [Ecology of hole-nesting birds of the Primor'ye.]
Poole, E. L. 1964. Pennsylvania birds.
Popov, V. A. (ed.). 1977. Ptitsy Volzhsko-Kamskogo kraia: nevorob inye. [Birds of the Volga and Kama valleys.]
Porter, E. 1972. Birds of North America: a personal selection.
———. 1977. Moments of discovery: adventures with American birds.
Porter, G. S. 1907. What I have done with birds.
———. 1920. Homing with the birds.
Porter, R. F. et al. 1976. Flight identification of European raptors.
Pough, R. H. 1946. Audubon bird guide. Eastern land birds.
———. 1951. Audubon water bird guide.
———. 1957. Audubon western bird guide.
Poznanin, L. P. 1978. Ekologicheskie aspekty evoliutsii ptits. [Ecological aspects of the evolution of birds.]
Pratt, A. 1937. The lore of the Lyrebird.
Prestwich, A. A. 1963. I name this parrot.
Priest, C. D. 1929. A guide to the birds of southern Rhodesia and a record of their nesting habits.
Puchalski, W. 1956. W krainie łabędzia. [In the land of the swan.]
———. 1957. Wyspa kormoranów. [The isle of the cormorants.]
Pulich, W. M. 1961. Birds of Tarrant County.
———. 1976. The Golden-cheeked Warbler.
Pycraft, W. P. (ed.). 1931. The standard natural history from amoeba to man.
Quarles, E. A. 1916. American pheasant breeding and shooting.
Queeny, E. M. 1946. Prairie wings.
Quilliam, H. B. R. 1973. History of the birds of Kingston, Ontario.
Raine, W. 1892. Bird-nesting in north-west Canada.
Rand, A. L. 1955. Stray feathers from a bird man's desk.
——— and E. T. Gilliard. 1967. Handbook of New Guinea birds.
Randolph, V. 1927. The ABC of biology.
Ratcliffe, D. A. 1980. The Peregrine Falcon.
Ravkin, I. S. 1978. Ptitsy lesnoĭ zony Priobia. [Birds of the forest region of the Ob River Valley.]
Reed, A. H. and A. W. Reed. 1955. New Zealand birds and flowers.
Reed, C. A. 1904, 1965. North American birds' eggs.
———. 1906. Bird guide—water birds, game birds and birds of prey.
———. 1908. Bird guide—land birds east of the Rockies.

———. 1912. American game birds.
———, H. F. Harvey, and R. I. Brasher. 1913. Western bird guide.
Reeves, H. M. 1975. A contribution to an annotated bibliography of North American cranes, rails, woodcock, snipe, doves and pigeons.
Regan, C. T. (ed.). 1937. Natural history.
Rehfus, R. (Compiler). 1968. California Condor (*Gymnogyps californianus*): the literature since 1900.
Reichenow, A. 1955. Vogelbilder aus Fernen Zonen Papageien.
Reichert, R. J. 1961. Binoculars and scopes.
Reĭmers, N. F. 1966. Ptitsy i mlekopitaiushchie iuzhnoĭ taĭgi Sredneĭ Sibiri. [Birds and mammals of the southern taiga of central Siberia.]
Rensch, B. 1959. Evolution above the species level.
Richardson, W. J. et al. 1975. Bird migration along the Beaufort Sea coast: radar and visual observations in 1975.
Richmond, W. K. 1934. Quest for birds.
Ridgely, R. S. 1976. A guide to the birds of Panama.
Ridgway, R. 1887. A manual of North American birds.
———. 1889. The ornithology of Illinois.
———. 1892. The hummingbirds.
——— and H. Friedman. 1901–1946. The birds of North and Middle America. Vols. 1–11.
Riley, J. H. 1938. Birds from Siam and the Malay Peninsula in the USNM collected by Drs. H. M. Smith and W. L. Abbott.
Riley, L. 1979. Guide to the national wildlife refuges.
Ripley, S. D. 1940. Trail of the money bird.
———. 1952. Search for the Spiny Babbler.
———. 1961. A synopsis of the birds of India and Pakistan.
———. 1977. Rails of the world.
———. (ed.). 1978. A bundle of feathers, proffered to Sálim Ali for his 75th birthday in 1971.
Risdon, D. H. S. 1957. An introduction to birdkeeping.
Ritter, W. E. 1938. The California Woodpecker and I.
Robbins, C. S., B. Bruun, and H. S. Zim. 1966. Birds of North America, a guide to field identification.
Roberts, A. 1940. The birds of South Africa.
———. 1978. Roberts' birds of South Africa.
Roberts, B. 1940. The life cycle of Wilson's Petrel.
———. 1940. The breeding behaviour of penguins.
———. 1941. A bibliography of Antarctic ornithology.
Roberts, T. S. 1919. A review of the ornithology of Minnesota.
———. 1932. The birds of Minnesota. Vols. 1, 2.
———. 1936. A manual for the identification of the birds of Minnesota and neighboring states.
———. 1937. 295 American birds.
———. 1938. Logbook of Minnesota bird life, 1917–1937.
Robertson, A. W. P. 1950. Birds: wild and free.
Robinson, B. L. and M. L. Fernald. 1908. Gray's new manual of botany.
Rodriguez, P. 1978. Panorama de la avifauna Colombiana.
Rogers, C. H. 1953. Care and breeding of budgies.
Romanoff, A. L. and A. J. Romanoff. 1949. The avian egg.

Rood, E. I. (ed.). 1896. 1893 World's congress on ornithology.
Roosevelt, T. 1910. African game trails.
Rorimer, I. T. 1940. A field key to our common birds.
Rossell, L. 1928. Tracks and trails.
Rourke, C. 1936. Audubon.
Rowan, W. 1931. The riddle of migration.
Royal Australasian Ornithologists' Union. 1926. Official checklist of the birds of Australia.
Roznowska-Feliksiakowa, Ciagłe. 1958. Wydawnictwa Ciage w Bibliotece Instytutu Zoologicznego Polskiej Akademii Nauk. [Periodicals in the library of the Zoological Institute of the Polish Academy of Sciences.]
Runcorn, S. K. (ed.). 1962. Continental drift.
Rüppell, G. 1975. Bird flight.
Russell, E. S. 1962. The diversity of animals.
Russell, F. 1964. Argen the gull.
Russia Ikhtiologicheskaia Komissia. 1965. Ryboiadnye ptitsy iikh znachenie v rybnom khoziastve. [Fish eating birds and their significance for the fish industry.]
Rutgers, A. 1967. Budgerigars in colour.
Rutter, R. J. (ed.). 1949. W. E. Saunders, naturalist.
Ryder, S. 1961. Blind Jack.
Ryves, B. H. 1948. Bird life in Cornwall.
Sage, J. H., L. B. Bishop, and W. P. Bliss. 1913. The birds of Connecticut.
Salomonsen, F. 1939. Moults and sequence of plumages in the Rock Ptarmigan.
——— and G. Johansen. 1950. Grønlands Fugle. Pts. 1–3.
Salt, W. R. 1973. Alberta vireos and warblers: families Vireonidae and Parulidae, distribution and breeding.
Samuels, E. A. 1883. Our northern and eastern birds.
Sandars, E. 1927. A bird book for the pocket.
Sanden, W. von. 1933. Guja: Leben am see der Vögel.
Sanderson, G. C. and J. C. Irwin. 1976. Effects of various combinations and numbers of lead: iron pellets dosed in wild-type captive Mallards.
Sanger, M. J. 1967. World of the Great White Heron.
———. 1969. Checkerback's journey: the migration of the Ruddy Turnstone.
Santos, E. 1948. Pássaros do Brasil.
Sarton, G. 1952. A guide to the history of science.
Sass, H. R. 1929. On the wings of a bird.
Saunders, A. A. 1921. A distributional list of the birds of Montana.
———. 1929. Bird song.
———. 1951. A guide to bird songs.
———. 1954. The lives of wild birds.
Saunders, H. 1899. An illustrated manual of British birds.
Saunders, R. M. 1947. Flashing wings.
Sawyer, E. J. 1930. Poems of nature and wild life.
Schaeffer, P. P. 1977. California Condor.
Schenk, E. T. and J. H. McMasters. 1936. Procedure in taxonomy.
Scherman, K. 1956. Spring on an arctic island.
Schinz, H. R. 1937. Beiträge zur Osteogenese des Knochensystems beim Haushuhn, bei der Haustaube und beim Haubensteissfus.
Schmalhausen, I. I. 1968. The origin of terrestrial vertebrates.
Schneider, E. 1955. All about parrakeets.
Schönwetter, M. 1974. Handbuch der Oologie. Vols. 1, 2.

Schorger, A. W. 1955. The Passenger Pigeon.
Schüz, E. 1959. Die Vogelwelt des Südkaspischen Tieflandes.
——— and H. Weigold. 1931. Atlas des Vogelzugs nach den Beringungsergebnissen bei palaearktischen Vögeln.
Schwartz, C. W. 1944. The Prairie Chicken in Missouri.
Scientific American. 1967. Psychobiology: the biological bases of behavior; readings from Scientific American.
Sclater, P. L. and O. Salvin. 1873. Nomenclator avium neotropicalium.
Sclater, W. L. 1912. A history of the birds of Colorado.
Scott, P. 1961. The eye of the wind.
——— and J. Fisher. 1954. A thousand geese.
Searing, G. F. et al. 1975. Seabirds of the southeastern Beaufort Sea: aircraft and group observations in 1972 and 1974.
Sears, P. B. 1937. This is our world.
Sebeok, T. A. 1968. Animal communication.
Seebohm, H. 1882. Siberia in Asia.
———. 1890. Classification of birds.
———. 1895. Supplement to Classification of birds.
Seeley, H. G. 1901. Dragons of the air.
Selous, E. 1933. Evolution of habit in birds.
Serle, W. and G. L. Morel. 1977. A field guide to the birds of West Africa.
Serventy, D. L. and H. M. Whittell. 1948, 1951. A handbook of the birds of western Australia.
———, V. Serventy, and J. Warham. 1971. The handbook of Australian seabirds.
Sharland, M. 1958. Tasmanian birds.
Sharp, D. L. 1926. Sanctuary! Sanctuary!
Sharpe, R. B. 1894. A hand-book to the birds of Great Britain. Vol. 1.
Sharrock, J. T. R. 1977. Atlas of breeding birds in Britain and Ireland. [Atlas UM, overlays WOS.]
Shattuck, G. B. 1905. The Bahama Islands.
Shattuck, G. C. (ed.). 1935. Handbook of travel.
Shaw, L. 1916. Nature notes of the Pikes Peak region.
Sheldon, W. G. 1967. The book of the American Woodcock.
Shelford, V. E. (ed.). 1926. Naturalist's guide to the Americas.
Sherborn, C. D. 1922–33. Index animalium. Sect. 1; Sect. 2, Pts. 1–33.
Sherman, A. R. 1952. Birds of an Iowa dooryard.
Shestakova, G. S. 1971. Stroenie kryl'ev i mekhanika poleta ptits. [The structure of wings and the mechanics of bird flight.]
Shick, C. 1952. A study of pheasants on the 9,000 acre prairie farm, Saginaw County, Michigan.
Shimomura, K. 1938. Genshoku yagai chôrui zufu. [Illustrated catalogue of field birds in color.]
Shinn, H. B. and G. A. Abbott. 1912. The North American bird and nature study manual.
Shiras, G. 1935. Hunting wild life with camera and flashlight. Vols. 1, 2.
Shortt, T. M. 1977. Wild birds of the Americas.
Shufeldt, R. W. 1890. The myology of the raven.
———. 1902. The osteology of the steganopodes.
———. 1909. Osteology of birds.
Sibley, C. G. 1955. A synopsis of the birds of the world.
Siegfried, W. R. et al. 1976. South African red data book—Aves.
Silloway, P. M. 1897. Sketches of some common birds.

Simmons, G. F. 1925. Birds of the Austin region.
Simon, E. 1921. Histoire naturelle des Trochilidae.
Simpson, G. G. 1976. Penguins: past, present, here and there.
Skead, C. J. (ed.). 1960. The canaries, seedeaters and buntings of southern Africa.
Skinner, M. P. 1928. A guide to the winter birds of the North Carolina sandhills.
Skutch, A. F. 1954, 1960, 1969. Life histories of Central American birds. I–III.
———. 1967. Life histories of Central American Highland birds.
———. 1971. A naturalist in Costa Rica.
———. 1973. The life of the hummingbird.
———. 1976. Parent birds and their young.
———. 1980. A naturalist on a tropical farm.
Sladen, W. J. L. 1958. The pygoscelid penguins.
Slater, P. 1975. A field guide to Australian birds. Passerines.
Sluckin, W. 1965. Imprinting and early learning.
Slud, P. B. 1964. The birds of Costa Rica: distribution and ecology.
Small, A. 1974. The birds of California.
Smith, D. 1880. Sir Andrew Smith's miscellaneous ornithological papers.
——— and R. Easton. 1964. California Condor, vanishing American.
Smith, D. R. 1975. Proceedings of the symposium on management of forest and range habitats for nongame birds.
Smith, R. C. 1946, 1952. Guide to the literature of the zoological sciences.
Smith, S. 1950. The Yellow Wagtail.
——— and E. Hosking. 1955. Birds fighting.
Smithe, F. B. 1974. Naturalist's color guide and supplement. Pts. 1, 2.
Smithe, G. 1931. A year of adventure with the birds.
Smithers, R. H. et al. 1957. A check list of the birds of southern Rhodesia.
Snow, D. W. 1958. A study of blackbirds.
Snyder, L. L. 1957. Arctic birds of Canada.
Sociedad de Ciencias Naturales La Salle. 1953. La región de Perijá y sus habitantes.
Soderberg, P. M. 1956. Foreign birds for cage and aviary. Vols. 1–4.
Soper, J. D. 1930. The Blue Goose.
South Africa National Parks Board of Trustees. 1958. Birds of the Kruger and other national parks. Vols. 1–4.
Southeastern Association of Game and Fish Commissioners. 1957. Mourning Dove investigations 1948–56.
Sowls, A. L. et al. 1978. Catalog of Alaskan seabird colonies.
Sparks, J. 1970. Bird behavior.
——— and T. Soper. 1967. Penguins.
Spasskaia, L. P. and A. A. Spasskii. 1977. Tsestody ptits SSSR; dilepididy sukhoputnykh ptits. [Cestodes of the birds of the USSR; Dilepidids of land birds.]
Sprunt, A., Jr. 1954. Florida bird life.
——— and E. B. Chamberlin. 1949. South Carolina bird life.
Squire, L. 1938. Wildfowling with a camera.
Stanford, J. K. 1949. The awl-birds.
Stanley, J. 1963. The essence of biometry.
Stearns, W. and E. Coues. 1887. New England bird life. Vol. 1.
Stebbins, G. L. 1966. Processes of organic evolution.
Stefferud, A. (ed.). 1966. Birds in our lives.
Stejneger, L. 1885. Results of ornithological explorations in the Commander Islands and in Kamtschatka.
———. 1936. Georg Wilhelm Steller.

Štepánek, O. 1959[?] Birds of field and forest.
Stepanian, L. S. 1975, 1978. Sostav i raspredelenie ptits fauny SSSR. [Composition and distribution of bird fauna of the USSR.] Vols. 1, 2.
Stephan, B. 1979. Urvögel. Archaeopterygiformes.
Stephens, T. C. 1945. An annotated bibliography of South Dakota ornithology.
Stevens, R. O. 1944. Talk about wildlife for hunters, fishermen, and nature lovers.
Stevenson, H. M. 1960. A key to Florida birds.
Stewart, R. E. 1975. Breeding birds of North Dakota.
Steyn, P. 1973. Eagle days: a study of African eagles at the nest.
Stirrett, G. M. 1968. An annotated bibliography pertaining to Point Pelee National Park and the Point Pelee region of Ontario.
Stoddard, H. L. 1932. The Bobwhite Quail, its habits, preservation and increase.
Stokes, D. W. 1979. Guide to the behavior of common birds.
Stone, W. 1894. The birds of eastern Pennsylvania and New Jersey.
———. 1937. Bird studies at Old Cape May. Vols. 1, 2.
Stonehouse, B. 1953. The Emperor Penguin.
Stoner, D. 1932. Ornithology of the Oneida Lake region.
Storer, J. H. 1948. The flight of birds analyzed through slow-motion photography.
———. 1954. The web of life.
Stout, G. D., P. Matthiessen, R. V. Clem, and R. S. Palmer. 1967. The shorebirds of North America.
Strecker, J. K., Jr. 1912. The birds of Texas.
Street, P. B. 1956. Birds of the Pocono Mountains, Pennsylvania.
Stresemann, E. 1975. Ornithology from Aristotle to the present.
Stroud, R. 1933. Diseases of canaries.
Stupka, A. 1963. Notes on the birds of Great Smoky Mountains National Park.
Sturgis, B. B. 1928. Field book of birds of the Panama Canal Zone.
Sturkie, P. D. 1954. Avian physiology.
Sutcliffe, S. A. (ed.). 1979. Second North American conference on Common Loon research and management, proceedings.
Sutton, G. M. 1928. An introduction to the birds of Pennsylvania.
———. 1932. The exploration of Southampton Island, Hudson Bay.
———. 1934. Eskimo year.
———. 1936. Birds in the wilderness.
———. 1951. Mexican birds: first impressions.
———. 1961. Iceland summer.
———. 1967. Oklahoma birds.
———. 1971. High Arctic.
———. 1972. At a bend in a Mexican river.
———. 1977. Fifty common birds of Oklahoma and the southern great plains.
Svensson, L. 1975. Identification guide to European passerines.
Sveriges Ornitologiska Forening. 1949, 1951. Förteckning över Sveriges Fåglar.
Swainson, W. 1834. A preliminary discourse on the study of natural history.
———. 1835. A treatise on the geography and classification of animals.
———. 1840. On the habits and instincts of animals.
Swann, H. K. 1921–22. A synopsis of the accipitres.
Swarth, H. S. 1929. A systematic study of the Cooper Ornithological Club.
———. 1931. The avifauna of the Galapagos Islands.
Swennen, C. 1977. Laboratory research on sea-birds.
Swinton, W. E. 1975. Fossil birds.

Symons, R. D. 1967. Hours and the birds.
Takatsukasa, N. 1930. Kaidori shûsei. [Collected works on pet bird-breeding.]
———. 1941. Japanese birds.
Taschenberg, O. 1886. Bibliotheca Zoologica II. Vols. 1–8.
Taverner, P. A. 1919. Birds of eastern Canada.
———. 1926. Birds of western Canada.
———. 1934, 1938, 1947. Birds of Canada.
———. 1939. Canadian land birds.
———. 1939. Canadian water birds.
Taylor, W. P. and W. T. Shaw. 1927. Mammals and birds of Mount Rainier National Park.
Tchernov, E. 1968. A preliminary investigation of the birds in the Pleistocene deposits of Ubeidiya.
Tegetmeier, W. B. (ed.). 1874. Reprint of Boddaert's Table des planches enlumineez d'histoire naturelle.
Temple, S. A. (ed.). 1978. Endangered birds: management techniques for preserving threatened species.
Tenny, S. and A. A. Tenny. 1884. Natural history of animals.
Thayer, E. and V. Keyes. 1913. Catalogue of a collection of books on ornithology in the library of John E. Thayer.
Thienemann, J. 1930. Rossitten.
———. 1931. Vom Vogelzuge in Rossitten.
Thomas, R. 1952. Crip, come home.
Thomé, E. 1942. Die Salzberger Schwalbengeschichte.
Thompson, R. L. (ed.). 1971. The ecology and management of the Red-cockaded Woodpecker. Proceedings of a symposium at Okefenokee National Wildlife Refuge, Folkston, Georgia, 26–27 May 1971.
Thomsen, P. 1957. Johann Friedrich Naumann.
——— and P. Jacobsen. 1979. The birds of Tunesia.
Thomson, A. L. 1926. Problems of bird-migration.
———. 1927. Birds, an introduction to ornithology.
———. 1942, 1949. Bird migration.
———. (ed.). 1964. A new dictionary of birds.
Thomson, J. A. 1923. The biology of birds.
———. 1924. Everyday biology.
Thoreau, H. D. 1925. Thoreau's bird-lore.
Thorpe, W. H. 1961. Bird song.
Ticehurst, C. B. 1938. A systematic review of the genus *Phylloscopus*.
Tillisch, C. J. 1949. Falkejagten og dens historie. [Falconry and its history.]
Tinbergen, L. 1946. De Sperwer als Roofvijand van Zangvogels. [The Sparrow Hawk as a predatory enemy of the songbird.]
Tinbergen, N. 1951. The study of instinct.
———. 1953. The Herring Gull's world.
———. 1953. Social behaviour in animals, with special reference to vertebrates.
——— and H. Falkus. 1907. Signals for survival.
Todd, W. E. C. 1940. Birds of western Pennsylvania.
———. 1963. Birds of the Labrador Peninsula.
——— and M. A. Carriker, Jr. 1922. The birds of the Santa Marta region of Colombia.
Torrey, B. 1901. Everyday birds.
Tout, W. 1947. Lincoln County birds.
Townsend, C. W. 1905. The birds of Essex County, Massachusetts.

———. 1920. Supplement to the birds of Essex County.
Trafton, G. H. 1910. Methods of attracting birds.
Trautman, M. B. 1940. The birds of Buckeye Lake, Ohio.
Trelease, S. F. and E. S. Yule. 1936. Preparation of scientific and technical papers.
Trimble, S. A. 1975. Non-game birds of the west: an annotated bibliography.
Trumbull, G. 1888. Names and portraits of birds which interest gunners.
Truslow, F. K. 1979. The nesting season: the bird photographs of Frederick Kent Truslow.
Tubbs, C. R. 1974. The buzzard.
Tuck, L. M. 1960. The murres.
———. 1972. The snipes.
Tufts, R. W. 1961. The birds of Nova Scotia.
Tunnicliffe, C. F. 1945. Bird portraiture.
———. 1979. A sketchbook of birds.
Turner, E. L. 1935. Every garden a bird sanctuary.
——— and P. H. Bahr. 1907. The home-life of some marsh birds.
Turner, J. F. 1971. The magnificent Bald Eagle.
Turner, L. M. 1886. Contributions to the natural history of Alaska.
Turner, W. 1903. Turner on birds.
Turner, W. J. (ed.). 1956. Nature in Britain.
Uchida, S. 1949. Nihon chōrui zusetsu. [New illustrations of the birds of Japan.]
———. 1953. Genshoku shōnen dōbutsu zukan. [Students' colored handbook of animals.]
——— and K. Shimomura. 1930. Photographs of bird-life in Japan. Vol. 1.
Uexküll, J. J. and G. Kriszat. 1934. Streifuzüge durch die Umwelten von Tieren und Menschen.
U.S. Department of Agriculture. 1956. Animal diseases.
U.S. Department of the Interior, Fish and Wildlife Service. 1975. Final environmental statement for the issuance of annual regulations permitting the sport hunting of migratory birds.
———. 1976. Operation of the National Wildlife Refuge System.
———. Bureau of Land Management. 1975. Snake River birds of prey research project annual report 1975.
U.S. Geographical Survey West of the 100th Meridian. 1871–1973. Report upon ornithological specimens.
U.S. Naval Astronomical Expedition. 1849–52. Vol. 2. Report of journeys across the Andes and pampas of the Argentine provinces.
Uspenskii, S. M. 1958. Birds of the Soviet arctic.
———. 1969. Zhizn' v vysokikh shirotakh. [Life in the high latitudes.]
Uttendörfer, O. et al. 1952. Neue Ergebnisse über die Ernährung der Greifvögel und Eulen.
van der Klaauw, C. J. 1963. Projections, deepenings and undulations of the surface of the skull in relation to the attachment of muscles.
Van Rossem, A. J. 1945. A distributional survey of the birds of Sonora, Mexico.
Van Tets, G. F. 1963. A comparative study of some of the social communication patterns of cormorants and related birds in the Pelecaniformes.
Van Tyne, J. and A. J. Berger. 1959, 1976. Fundamentals of ornithology.
Van Vleck, S. 1963. Growing wings.
Vaurie, C. 1959, 1965. The birds of the palearctic fauna. Vol. 1, Passeriformes; Vol. 2, Non-passeriformes.
Vichitich, V. N. 1939. Seasonal distribution and migration of ducks (Subfamily Anatinae) on the base of bird ringing in the U.S.S.R. Vol. 3.
Villafañe, J. 1957. Historias de pájaros.

Vincent, J. 1952. A check list of the birds of South Africa.
Vladyshevskii, D. V. 1975. Ptitsy v antropogennom landshafte. [Birds in a landscape affected by man.]
———. 1980. Ekologiya lesnykh ptits i zverei (Kormodobyranie i ego biotsenoticheskoe znachenie). (Ecology of forest birds and animals (Foraging and its ecosytematic importance).]
Voigt, A. 1913, 1950. Exkursionsbuch zum Studium der Vogelstimmen.
Voous, K. H. 1947. The history of the distribution of the genus *Dendrocopos*.
———. 1962. Die Vogelwelt Europas und ihre Verbreitung.
———. 1977. List of recent holarctic bird species.
Vorobev, K. A. 1963. Ptitsy Iakutii. [Birds of Yakutia.]
Voronin, R. N. 1978. Belaya Kuropatka Bel'shez emel'koi tundry; ekologiya, morfologiya, khozyaistvennoc ispol'zavanie. [The Willow Grouse (*L. lagopus*) of the Bol'shezmel'skii tundra; ecology, morphology and economic utilization.]
Waddington, C. H. 1952. The epigenetics of birds.
Walker, J. J. (ed.). 1934. The natural history of the Oxford district.
Walker, R. S. 1955. As the indians left it.
Walkinshaw, L. 1973. Cranes of the world.
———. 1977. Life history of the Eastern Field Sparrow in Calhoun Co., Michigan.
Wallace, A. R. 1876. The geographical distribution of animals. Vols. 1, 2.
———. 1881. Island life.
Wallace, G. J. 1939. Bicknell's Thrush, its taxonomy, distribution and life history.
———. 1977. Birds of the Lake Michigan drainage basin.
———. 1979. My world of birds.
——— and H. D. Mahan. 1955, 1975. An introduction to ornithology.
Walls, G. L. 1942. The vertebrate eye and its adaptive radiation.
Walter, H. E. and A. H. Walter. 1906, 1910. Wild birds in city parks.
Wardlaw Ramsay, R. G. 1923. Guide to the birds of Europe and North Africa.
Warren, B. H. 1888. Report on the birds of Pennsylvania.
———. 1890. Birds of Pennsylvania.
Washburn, M. F. 1926. The animal mind.
Waterton, C. 1891. Wanderings in South America.
Watkinson, E. 197? A guide to birdwatching in Mallorca.
Watson, A. D. 1977. The Hen Harrier.
Watson, G. E. 1966. Seabirds of the tropical Atlantic Ocean.
———. 1975. Birds of the Antarctic and Sub-Antarctic.
———, R. L. Zusi, and R. W. Storer. 1963. Preliminary field guide to the birds of the Indian Ocean.
Wauer, R. H. 1973. Birds of Big Bend National Park and vicinity.
Wayne, A. T. 1910. Birds of South Carolina.
Wdowiński, Z. 1955. Amidst forests and lakes.
Webb, C. S. 1954. The odyssey of an animal collector.
Webster, M. 1976. A new guide to the birds of Hong Kong.
Weed, C. M. 1904. Bird life stories. Book 1.
——— and N. Dearborn. 1903. Birds in their relations to man.
Weigold, H. 1930. Der Vogelzug auf Helgoland.
Weiss, H. B. and G. M. Ziegler. 1931. Thomas Say; early American naturalist.
Welker, R. H. 1955. Birds and men.
Weller, M. W. 1980. The island waterfowl.
Wellman, P. I. 1957. Portage Bay.

Welty, J. C. 1962. The life of birds.
Wenzel, F. 1959. The buzzard.
Wetmore, A. 1916. Birds of Porto Rico.
———. 1930. The migrations of birds.
———. 1931. Birds.
———. 1964. Song and garden birds of North America.
———. 1965, 1972. The birds of the Republic of Panama. Pts. 1–3.
———. 1966. Water, prey and game birds of North America.
Wheaton, J. M. 1882. Report on the birds of Ohio.
Wheeler, W. M. 1928. Emergent evolution and the development of societies.
Wheelock, I. G. 1912. Birds of California.
Whistler, H. 1928, 1935, 1949. Popular handbook of Indian birds.
White, G. 1899. The natural history of Selborne.
White, T. H. 1951. The Goshawk.
Whitney, N. R., Jr. 1978. The birds of South Dakota.
Whittell, H. M. 1954. The literature of Australian birds.
Wight, H. M. 1933. Suggestions for pheasant management in southern Michigan.
Williams, C. S. 1967. Honker.
Williams, G. R. 1963. Birds of New Zealand.
Williams, H. S. 1939. The private lives of birds.
Williams, J. 1951. The fall of the sparrow.
Williams, J. G. 1963. A field guide to the birds of east and central Africa.
Wilson, A. 1852. Wilson's American ornithology.
Wilson, E. 1967. Birds of the Antarctic.
Winterbottom, J. M. 1951. Common birds of the Cape.
Wirth, H. (ed.). 1968. Geschützte Natur.
Witherby, H. F. et al. 1938–1941. The handbook of British birds. Vols. 1–5.
Wolfson, A. (ed.). 1955. Recent studies in avian biology.
Won, P-O. 1969. An annotated checklist of the birds of Korea.
Wood, C. A. 1917. The fundus oculi of birds especially as viewed by the ophthalmoscope.
———. 1931. An introduction to the literature of vertebrate zoology.
Wood, J. G. 1872. The illustrated natural history. Birds.
Wood, M. 1967. Birds of Pennsylvania.
———. 1969. A bird-bander's guide to determination of age and sex of selected species.
Wood, N. 1951. The birds of Michigan.
Wood, S. 187[?]. The British bird-preserver.
Wood, T. W. [?] Curiosities of ornithology.
Woodruff, F. M. 1907. The birds of the Chicago area.
Worden, A. N. 1956. Functional anatomy of birds.
Wright, H. W. 1909. Birds of the Boston Public Garden: a study in migration.
Wyman, L. E. and E. F. Burnell. 1925. Field book of the birds of the southwestern United States.
Wynne, O. E. 1956. Key-list of the palaearctic and oriental passerine birds.
Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behavior.
Yamashina Institute (ed.). 1975. Kono tori o mamorō. [Let's preserve these birds in Japan.]
Yamashina, Y. 1961, 1974. Birds in Japan, a field guide.
Yapp, W. B. 1962. Birds and woods.
Yarrow, H. C. and H. W. Henshaw. 1874. Report upon ornithological specimens collected in the years 1871–1873.
Yeates, G. K. 1934. The life of the Rook.

Youth's Cabinet. 1858. Vol. 1. The birds.
Zahl, P. A. 1956. Coro-Coro. The world of the Scarlet Ibis.
Zaslavskii, M. A. 1966. Izgotovlenie chuchel ptits. [Preparation of bird mounts, skeletons and museum preparations.]
Zedtwitz, F. X. 1933. Vogelkinder der Waikariffe.
Zeleny, L. 1976. The bluebird: how you can help its fight for survival.
Zimmer, J. T. 1926. Catalogue of the Edward E. Ayers ornithological library. Pts. 1, 2.
Zimmerman, D. R. 1975. To save a bird in peril.
Zimmerman, K. 1952. Vergleichende Farbtabellen. [Comparing colour plates. Ridgway—Ostwald, Ostwald—Ridgway.]

PRESIDENT'S MESSAGE

In last year's June issue of The Wilson Bulletin, I announced that the Society would seek funds for the endowment of the Louis Agassiz Fuertes and Margaret Morse Nice awards. Subsequently, Dr. C. John Ralph prepared a direct mail solicitation. The response to this solicitation, together with donations included with the annual dues notice provided more than $7000. This sum is sufficient to insure both the permanency and prestige of the awards. Further, we will now be able to give two awards in each category.

Many past winners of the awards, some now famous, provided testimonials for the circular. While reading these, I was struck by the frequent statement that what really counted was not the prize money, but the recognition by peers that the work was worthwhile. This has strengthened my conviction that the encouragement of amateurs and students is one of the Society's most important functions.

I would like to extend my personal thanks to each of you who helped make this campaign a success. Special thanks are due to our Canadian members who, despite stringent tax laws, were so generous.

Abbot S. Gaunt
President

WINNERS OF THE LOUIS AGASSIZ FUERTES AWARD
1947–1982

1947	L. Richard Mewaldt
1948	no award
1949	Stephen W. Eaton
1950	Henry E. Childs
	Bryon E. Harrell
	Arnold J. Petersen
	Harrison B. Tordoff
1951	Howard L. Cogswell
1952	Robert W. Nero
1953	no award
1954	William C. Dilger
1955	Robert G. Wolk
1956	John Burton Miller
	Lester L. Short
1957	Millicent S. Ficken
1958	Harold D. Mahan
1959	no award
1960	Robert T. Lynn
1961	Frances C. James
1962	Donald S. Heintzelman
1963	Nickolas A. M. Verbeek
1964	Robert E. Gobeil
1965	John O. Sullivan
1966	Douglas D. Dow
	Ralph W. Schreiber
1967	Dennis L. Kolma
	Spencer G. Sealy
1968	Leon John Gorshi
	James M. Utter
1969	Richard E. John
	G. Fredrick Stanholtzer
1970	Thomas C. Dunstan
1971	Flash Gibson
1972	Donald E. Kroodsma
1973	Robert C. Eckhardt
1974	David S. Dobkin
1975	Roger L. Boyd
	Margaret Elsie McVey
1976	Richard O. Bierregaard, Jr.
1977	Dale Lewis
	Ernest E. Stevens
1978	Alexis A. E. McLean
1979	Patricia Gowaty
1980	Gregory S. Butcher
1981	Mark K. Wourms
1982	Brian J. McCaffery
	Stephen Nowicki

ORNITHOLOGICAL NEWS

THE WILSON ORNITHOLOGICAL SOCIETY ANNOUNCES AWARDS

Louis Agassiz Fuertes, Margaret Morse Nice, and Paul A. Stewart Awards

Fuertes Awards are available to all ornithologists, although graduate students and young professionals are preferred. Any kind of avian research may be funded. One or two awards of at least $200 may be presented.

Nice Awards are limited to independent researchers without access to funds and facilities available at colleges, universities, or governmental agencies, and are thus restricted to amateurs, including high school students. Any kind of avian research may be funded. One, rarely two, awards of at least $200 may be presented.

Stewart Awards are available to any ornithologist. Preference will be given to studies of bird movements based on banding, analysis of recoveries, and returns of banded birds, or economic ornithology. Several awards of $200 are presented.

Applicants **must** use the Research Awards Application Form, which can be obtained by writing to W. O. S. Research Awards, Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109. A condition of all the awards is willingness to report the results of the research as either an oral or poster presentation at one of the Society's annual meetings. Completed applications must be received before 1 March 1983.

Aaron M. Bagg Student Membership Awards

Student membership awards in The Wilson Ornithological Society are available for persons not currently members of the Society because of funds generously donated in the memory of Aaron M. Bagg, a former president of the Society. This award provides a 1-year membership in The Wilson Ornithological Society for successful nominees. Application forms for the awards to be granted in 1983 may be obtained from John L. Zimmerman, Division of Biology, Kansas State University, Manhattan, Kansas 66506. The deadline for applying is 1 November 1982.

WILSON SOCIETY 64TH ANNUAL MEETING

The **64th Annual Meeting** of The Wilson Ornithological Society will be held **2–5 June 1982** at the University of Wisconsin-Green Bay, Green Bay, Wisconsin. Persons desiring to organize mini-symposia or be on the scientific program should contact Clait E. Braun, Wildlife Research Center, 317 West Prospect, Fort Collins, Colorado 80526.

ANNUAL RAPTOR MEETING

The annual meeting of the Raptor Research Foundation will be held 18–21 November 1982 at the Hotel Utah in Salt Lake City. Contact James A. Gessaman, UMC 53, Utah State University, Logan, Utah 84322 for information regarding the scientific program. Deadline for receipt of abstracts is 15 September 1982. Contact Stellanie Ure, % The Raptor Society, 19 Exchange Place, Salt Lake City, Utah 84111 for registration information.

This issue of *The Wilson Bulletin* was published on 28 September 1982.

The Wilson Bulletin

Editor Jon C. Barlow

Department of Ornithology
Royal Ontario Museum
100 Queen's Park
Toronto, Ontario, Canada M5S 2C6

Associate Editor Margaret L. May

Assistant Editors Gary Bortolotti
Nancy Flood
Keith L. Bildstein

Senior Editorial Assistant Richard R. Snell

Editorial Assistants C. Davison Ankney
James D. Rising

Review Editor Robert Raikow
Department of Biological Sciences
University of Pittsburgh
Pittsburgh, PA 15260

Color Plate Editor William A. Lunk
865 North Wagner Road
Ann Arbor, MI 48103

Suggestions to Authors

See Wilson Bulletin, 91:366, 1979 for more detailed "Suggestions to Authors." Manuscripts intended for publication in *The Wilson Bulletin* should be submitted in triplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411–419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

Notice of Change of Address

If your address changes, notify the Society immediately. Send your complete new address to Ornithological Societies of America, Cornell Laboratory of Ornithology, 159 Sapsucker Woods Rd., Ithaca, New York 14850.

The permanent mailing address of the Wilson Ornithological Society is: c/o The Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109. Persons having business with any of the officers may address them at their various addresses given on the back of the front cover, and all matters pertaining to the Bulletin should be sent directly to the Editor.

Membership Inquiries

Membership inquiries should be sent to Dr. Keith Bildstein, Department of Biology, Winthrop College, Rock Hill, South Carolina 29733.

CONTENTS

SYSTEMATIC RELATIONSHIPS AND ZOOGEOGRAPHY OF THE WHITE-WINGED GUAN (*PENELOPE ALBIPENNIS*) AND RELATED FORMS ---------- *J. William Eley* 241

ON THE MATING SYSTEM OF BROWN-HEADED COWBIRDS ---- *C. Davison Ankney and D. M. Scott* 260

KLEPTOPARASITISM BY SOUTH POLAR SKUAS ON BLUE-EYED SHAGS IN ANTARCTICA
Stephen J. Maxson and Neil P. Bernstein 269

INTRASPECIFIC FOOD ROBBING IN GLAUCOUS-WINGED GULLS ------ *Elizabeth Drexler Rockwell* 282

EFFECT OF FOREST STRUCTURE ON AMERICAN REDSTART FORAGING BEHAVIOR
George E. Seidel and Robert C. Whitmore 289

FACTORS INFLUENCING WINTER DISTRIBUTION AND ABUNDANCE OF TOWNSEND'S SOLITAIRE
Carl E. Bock 297

MIGRATION PATTERNS OF RED AND NORTHERN PHALAROPES IN SOUTHWEST DAVIS STRAIT AND IN THE NORTHERN LABRADOR SEA
Craig D. Orr, Richard M. P. Ward, Norman A. Williams, and R. G. B. Brown 303

RECRUITMENT AND SOCIALLY-SPECIFIC FLOCKING TENDENCIES OF EASTERN SANDHILL CRANES
James R. Lovvorn and Charles M. Kirkpatrick 313

EFFECTS OF CONTEXTUAL INFORMATION ON BEHAVIOR OF *CALIDRIS* SANDPIPERS FOLLOWING ALARM CALLS ---------- *Daniel W. Leger and Jami L. Nelson* 322

NEST-SITE SELECTION BY CAVITY-NESTING BIRDS OF RIPARIAN HABITATS IN IOWA
Dean F. Stauffer and Louis B. Best 329

NESTS, TERRITORIES, AND REPRODUCTION OF SEDGE WRENS (*CISTOTHORUS PLATENSIS*)
Jeffrey T. Burns 338

GENERAL NOTES

NOTES ON MIGRANTS WINTERING AT MONTEVERDE, COSTA RICA
Elliot J. Tramer and Thomas R. Kemp 350

DECLINE OF THE ROADRUNNER IN MISSOURI ------ *Douglas J. Norris and William H. Elder* 354

THE OCCURRENCE AND BEHAVIOR OF NON-BREEDING HORNED PUFFINS AT BLACK GUILLEMOT COLONIES IN NORTHERN ALASKA ---------- *George J. Divoky* 356

BODY TEMPERATURE AND GROWTH OF BONIN PETREL CHICKS
Ted N. Pettit, Gilbert S. Grant, and G. Causey Whittow 358

PROLONGED INCUBATION BEHAVIOR IN COMMON LOONS ---------- *Scott Sutcliffe* 361

BARN SWALLOW FLEDGLING SUCCESSFULLY ELICITS FEEDING AT A NON-PARENTAL NEST
Gregory Ball 362

COWBIRD CONTROL AND ITS EFFECT ON KIRTLAND'S WARBLER REPRODUCTIVE SUCCESS
Sean T. Kelly and Michael E. DeCapita 363

UNUSUAL NEST SANITATION BY A BROAD-WINGED HAWK
Robert N. Rosenfield, Adam J. Rosenfield, and Michael W. Gratson 365

FIRST RECORD OF A BALD EAGLE NEST IN WEST VIRGINIA
Maurice N. LeFranc, Jr., Thomas A. Pierson, and Michael G. May 366

OSPREY SPREADS WINGS AFTER FISHING ---------- *A. M. Elowson-Haley* 366

ROUGH-WINGED SWALLOWS SCAVENGING ADULT MIDGES ---------- *Spencer G. Sealy* 368

DIET OF GLAUCOUS GULLS IN WESTERN ALASKA ---------- *Carl Strang* 369

VOCAL BEHAVIOR OF THE NORTHERN ORIOLE ---------- *L. David Beletsky* 372

DOCUMENTATION AND STATUS OF CORY'S SHEARWATER IN THE WESTERN GULF OF MEXICO ---------- *Warren Pulich, Jr.* 381

ORNITHOLOGICAL LITERATURE ---------- 386

LIST OF BOOKS IN THE JOSSELYN VAN TYNE MEMORIAL LIBRARY, THE WILSON ORNITHOLOGICAL SOCIETY ---------- 393

PRESIDENT'S MESSAGE ---------- 430

ORNITHOLOGICAL NEWS ---------- 259, 432

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 94, NO. 4 DECEMBER 1982 PAGES 433–650

MUS. COMP. ZOOL
LIBRARY
FEB 14 1983
HARVARD
UNIVERSITY

Adult Zapata Sparrow, *Torreornis inexpectata*.
Gouache-acrylic painting by John P. O'Neill.

THE WILSON BULLETIN
A QUARTERLY MAGAZINE OF ORNITHOLOGY
Published by the Wilson Ornithological Society

VOL. 94, NO. 4 DECEMBER 1982 PAGES 433–650

Wilson Bull., 94(4), 1982, pp. 433–446

THE BIOLOGY OF *TORREORNIS INEXPECTATA* I. A COMPARISON OF VOCALIZATIONS IN *T. I. INEXPECTATA* AND *T. I. SIGMANI*

EUGENE S. MORTON AND HIRAM J. GONZALEZ ALONSO

The Zapata Finch (*Torreornis inexpectata*) is endemic to Cuba in three remarkably different habitats. The first population, consisting today of about 250 individuals, was discovered in the Zapata Swamp near the town of Santo Tomas, in 1926 (Barbour and Peters 1927). The second population (*T. i. sigmani*), separated by 720 km from the Zapata Swamp was not discovered until 1959 (Spence and Smith 1961) and inhabits the driest area in Cuba, a coastal zone dominated by the shrub called coastal incense (*Tournefortia gnaphalodes*) near the town of Baitiquiri on the southeastern tip of Cuba (Fig. 1). This population consists of 55–100 pairs. A third population (*T. i. varonai*), discovered in semideciduous dry forest and thorn scrub on Cayo Coco on the northern coast in the mid-1970's, has recently been described (Regalado 1981).

Little was known about the biology of the first two populations until two expeditions, of which the authors were members, by the Instituto de Zoologia of the Cuban Academy of Sciences studied various aspects of the ecology and behavior of the species. This report emphasizes the acoustic communication of *Torreornis*; future publications will cover the species' ecology, demography, conservation, and natural history.

Torreornis is thought to be related to the emberizine genus *Aimophila* (Paynter and Storer 1970). The rufescent crown and black malar stripe do resemble these features in some members of that genus (see frontispiece). The subspecies of *Torreornis* are similar in size, but the eastern population is much duller, with the rufous on the crown and the yellow of the breast less intense, than those finches found in the humid Zapata Swamp. The emberizine finches are well known for inter-populational song differences. Through song learning, local song dialects may develop (Marler and Ta-

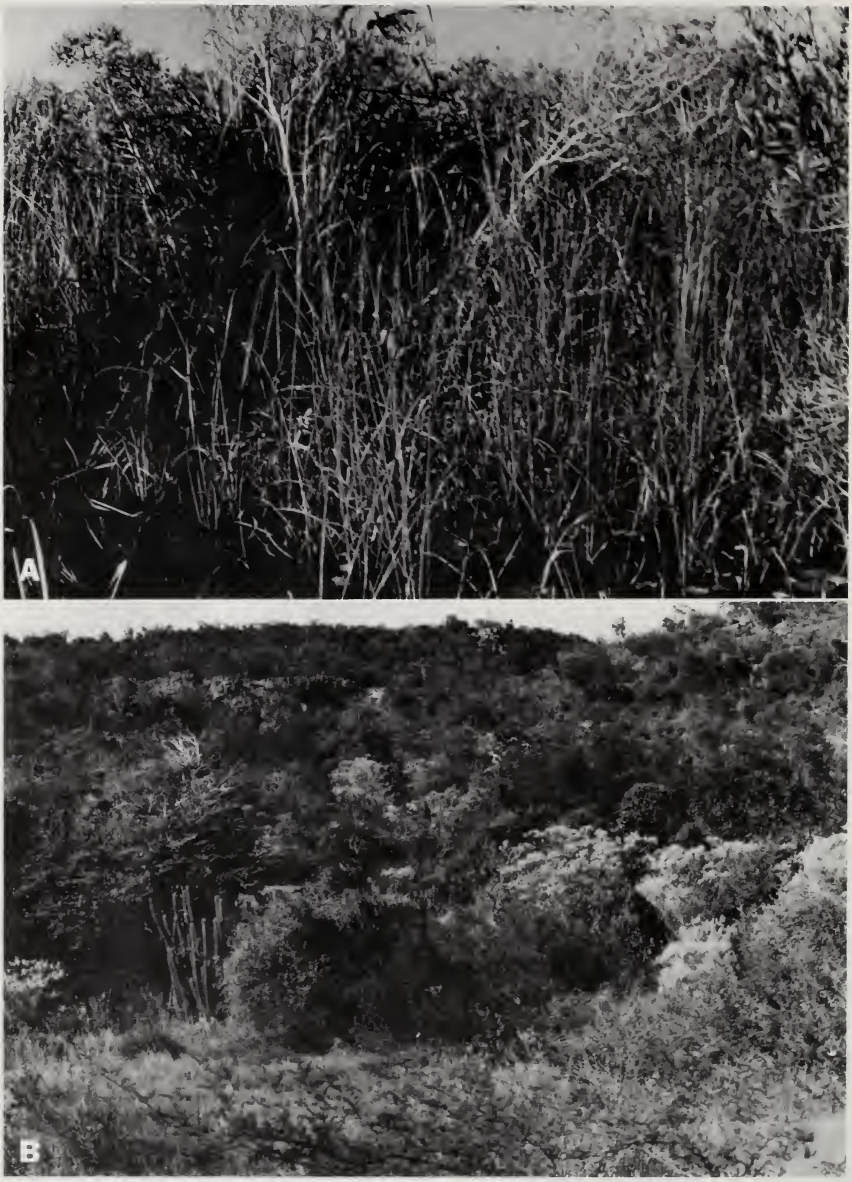


FIG. 1. Habitats of *T. inexpectata*. (A) *Myrica* and sawgrass hummock surrounded by water used by *T. i. inexpectata* in the Zapata Swamp. (B) Dense cactus and thorn scrub habitat of *T. i. sigmani* 5 km W of Tortuguilla. *Torreornis* habitat is indicated by the light colored leaves of coastal incense (*Tournefortia gnaphalodes*), right center; *Torreornis* eats its small seed pods.

mura 1964), especially if the populations are non-migratory (Baptista 1976). Differences in the acoustics of habitats may also select for differences in the types of sounds used in long distance communication. For example, forest birds tend to use clear tones, whereas birds of grassland and marshes use highly frequency-modulated sounds (Morton 1975). Thus, one might expect that populations of *Torreornis* living in a near-desert community (*T. i. sigmani*) would be under a different acoustical regime than *T. i. inexpectata* in its sawgrass, *Myrica* hummock-filled swamp habitat. The 720 km now separating these populations would insure that no recent contact might affect a resemblance in their vocalizations through cultural exchange. The purposes of this report, therefore, are to describe the vocal behavior of *Torreornis* and to compare and contrast the vocal behavior in the two populations.

METHODS

Recordings were made with a Uher 4000 Report tape recorder at a tape speed of 19 cm/sec with a Dan Gibson 46.2 cm diameter parabolic reflector. Sounds were analyzed on a Kay Elemetrics Company Sonagraph model 7029 using the wide band filter and with a Princeton Applied Research Real Time Spectrum Analyzer model 4512 coupled to a Unigon Scan Converter. All illustrations were made from sonagram traces.

Recordings were obtained of *T. i. inexpectata* during the "Expedition Florentino Garcia Montaña" to the Zapata Swamp from 25 October–1 November 1979; those of *T. i. sigmani* were made from 2–5 November 1980. Tape recordings of song and callnotes were used to elicit responses from pairs; playbacks of songs of *T. i. inexpectata* to individuals of *T. i. sigmani* resulted in prompt responses and song displays. Playbacks were used to lure pairs into mist nets for capture and color banding.

RESULTS

General behavior.—Torreornis exists in pairs that appear to defend territories throughout the year. Neither population was breeding during our study of vocal behavior, yet pairs responded to playback of the duet song by flying toward the sound, then perching conspicuously. Duets occurred when one bird, usually the male, flew to a new perch followed by the female. Immediately upon landing, the birds perched within 7–30 cm of one another and, with wings waving slowly, sang one of their forms of duet song (see below). When pair members were separated, the buzz callnote was given by either sex as a contact note. Often the first response to a song playback would be rapid chip notes as one bird flew toward the source of the sound. One bird from each population was recorded as it gave distress sounds upon being removed from a mist net. These then were the four general classes of vocalizations recorded from both populations of *Torreornis*: song (includes duet and single bird songs), chips, buzz calls, and distress call. *Torreornis* thus has a simple vocal repertoire although structural variation occurs within each of the four general classes

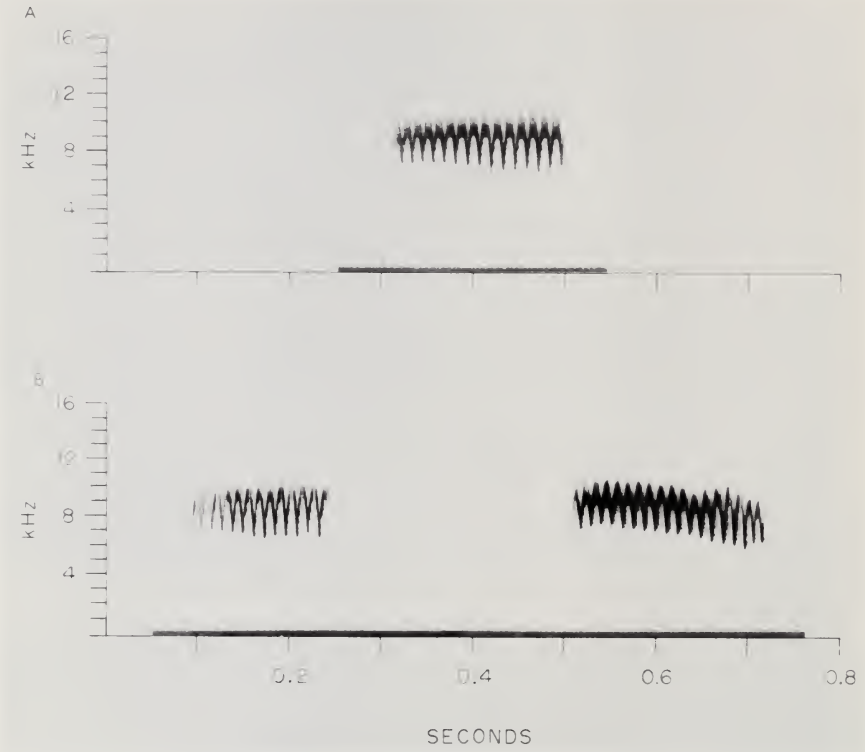


FIG. 2. Buzz callnotes of *T. i. inexpectata* (see text). This and all other figures are from wide band spectrograms.

of sounds. The duet was remarkably complex with respect to the timing of each pair-member's contribution to it and to changes in note structure during a single duet.

During the expedition to study *T. i. sigmani*, important differences between the sexes were noted that allowed us to sex birds in the field, even though the species is monomorphic. Males would nearly always precede females while the pair was responding to a song playback in their territory. Second, males often gave two to four contact buzz notes in a series, whereas females only gave single buzz notes. We do not know if the same holds true for *T. i. inexpectata*. The sexual difference for *T. i. sigmani* was confirmed for us after several birds were collected for specimens.

We now describe in more detail the variation in sound structure within each of the four vocalization classes.

The buzz call.—Buzz calls are illustrated in Fig. 2 for *T. i. inexpectata*

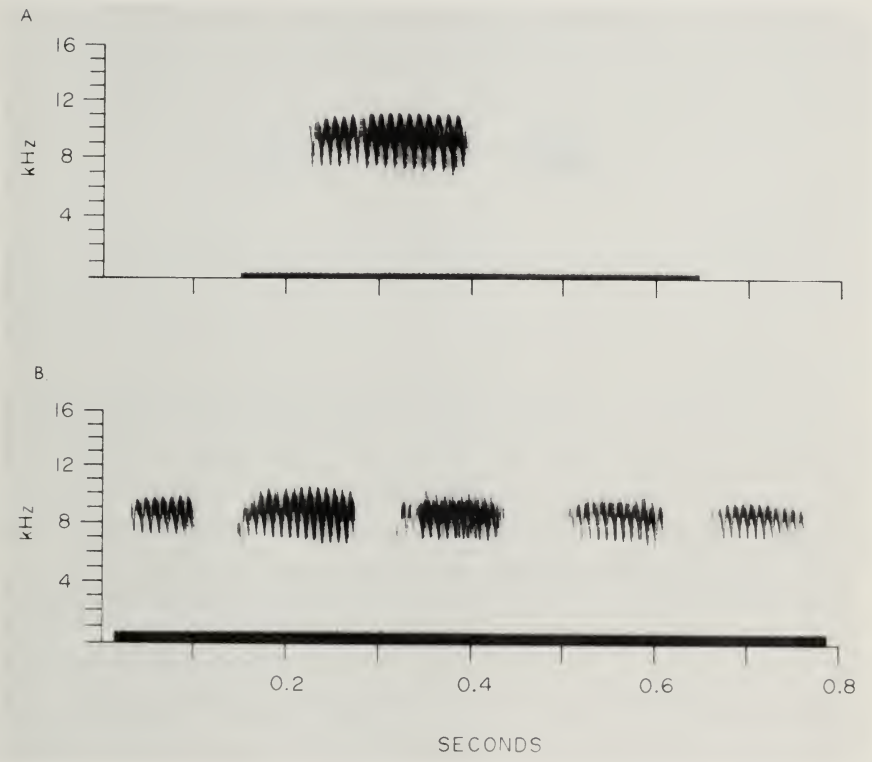


FIG. 3. Buzz callnotes of *T. i. sigmani* (see text).

and in Fig. 3 for *T. i. sigmani*. This is the most commonly heard sound and is the sound that betrays the presence of this difficult-to-see finch to the human observer. To the human ear it sounds like a high pitched *zeee* or *zeeea* of varying duration, but the spectrograms prove that it has a complex sound structure.

T. i. inexpectata buzz calls modulate in frequency between 5.3–10.9 kHz with a carrier frequency from 8–10 kHz. *T. i. sigmani* buzz calls range from 7.5–13 kHz with a carrier frequency at 9–10 kHz. There is also a difference in the modulation rate: *T. i. inexpectata* calls are modulated in frequency at a rate ranging from 90–100 Hz, whereas *T. i. sigmani* buzz calls are frequency modulated at a rate of from 110–120 Hz ($t = 12.1711$, $P < 0.001$). This difference is easily seen if Figs. 2 and 3 are compared; *T. i. sigmani* calls appear like a compressed spring while *T. i. inexpectata* calls look like a less compressed spring, reflecting the difference in modulating rates.

Although the modulation rate does not change during a buzz call, the frequency range of the modulation does change in some calls. In Figs. 2A and 3A. the frequency range of the modulation increases 1 kHz part way through the call. This is indicated by the sudden increase in the width of the spectrogram trace. The increase in frequency range is due to the inclusion of lower frequencies. not higher frequencies into the sweep of the modulation.

Buzz calls also vary in their rate of repetition (contrast Fig. 2B with Fig. 3B) and they may decrease in overall frequency (Fig. 2B at right) or they may rise and fall in frequency. All of these variations are easily apparent to the human listener. Individual buzz calls also ranged from 0.07–0.25 sec in duration.

These variations are associated with the nearness of the mate and whether or not the mate is also giving callnotes. A lone bird utters isolated buzz calls of long duration. If the mate appears to respond, the buzz calls tend to rise or to rise and fall in carrier frequency. Males in the *T. i. sigmani* population seemed to use series of three to five buzz calls more often than males of *T. i. inexpectata* (Fig. 3B).

Buzz calls were uttered while mates were foraging on the ground out of visual contact with one another and also during reactions to playbacks of tape recorded songs. The buzz calls appear to function to keep mates in contact and probably also function to keep family groups in contact. We never observed more than two birds together in the *T. i. sigmani* population. but *T. i. inexpectata* occurred in groups of three or four as well as in pairs at the same time of year. Perhaps the breeding season is later in the Zapata Swamp and family groups have not yet broken up. Ripley and Watson (1956) also found *T. i. inexpectata* in small groups in October. Since *Torreornis* reacts aggressively to played-back song, defending year-long territories (Gonzalez, pers. obs. of color banded birds), these groups are likely to consist of family groups rather than indicating a general social flocking tendency. It remains to be determined if *T. i. inexpectata* males have sex-characteristic series of buzz calls as do *T. i. sigmani* males.

Distress call.—Distress calls (Fig. 4A, *T. i. inexpectata*; Fig. 5A, *T. i. sigmani*) were recorded from one captured bird from each population. One free *T. i. sigmani* female gave distress calls identical in physical structure to those of the bird in Fig. 5A, when briefly attacked by her mate. Distress calls have a regular modulation in frequency at a rate of 60 cps in the *T. i. inexpectata* example, through a frequency range of about 4–9 kHz. They are short in duration (ca. 0.1 sec) and are delivered at variable rates. *T. i. sigmani* distress calls are not frequency modulated in a regular fashion. Distress calls in both populations differ from buzz calls in being lower in frequency and in having more abrupt changes in frequency at the maximum and minimum.

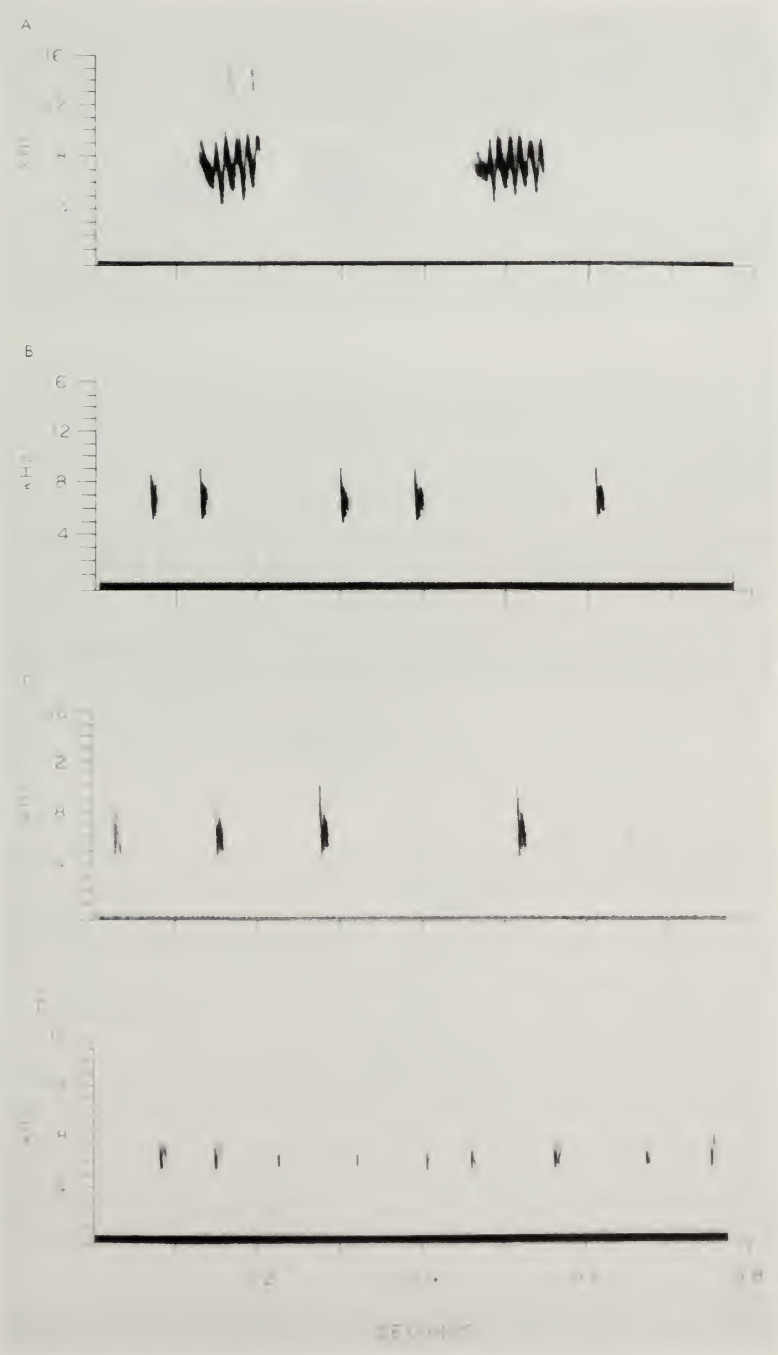


FIG. 4. A. Distress calls. B–D. Chips (*T. i. inexpectata*).

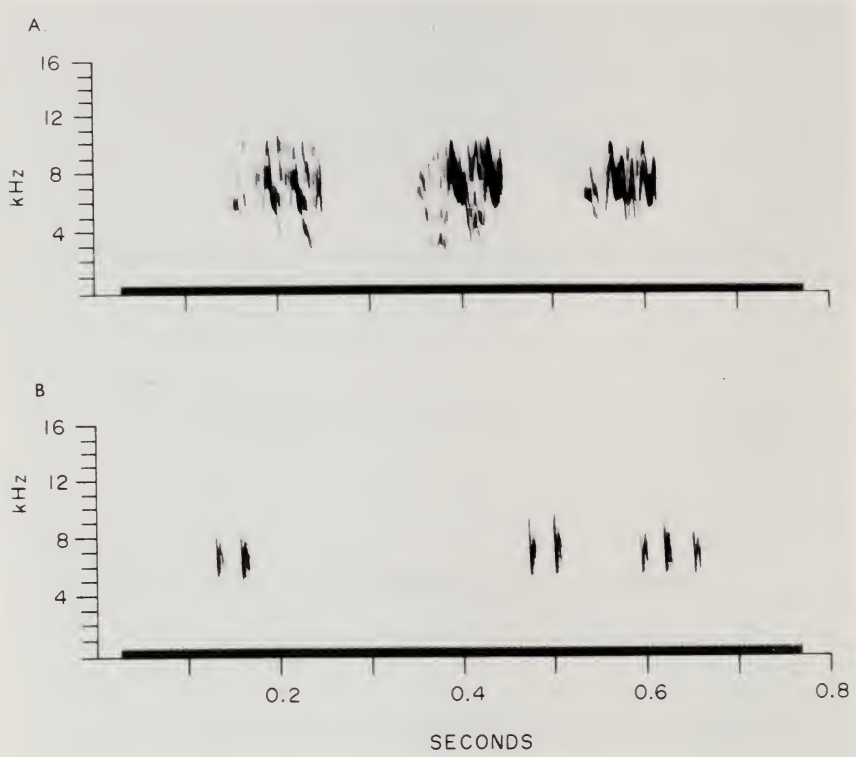


FIG. 5. A. Distress calls. B. Chips (*T. i. sigmani*).

Distress calls occur when a bird is unable to escape from a frightening stimulus as when captured by humans or attacked inadvertently by a mate looking for a territorial intruder. Whether the obvious differences in distress call structure in Fig. 4A and 5A reflect true differences between the populations is uncertain and must await a larger sample.

Chips.—Chips were identical in the two populations (Fig. 4B–D, *T. i. inexpectata*; Fig. 5B, *T. i. sigmani*). They varied greatly in rate, from single notes to rapid rates up to 20 per sec. Each chip consists of an initial rapid, pulse-like downswept frequency modulation followed by a chevron-shaped up-then-down frequency change, within about 0.01 sec. The frequency ranges of chips also varied. Chips were sometimes delivered rapidly in bouts of two or three as in Fig. 4B.

The rate of chip delivery appeared to vary directly with how aroused or stimulated the calling bird was. A bird responding to a played back re-

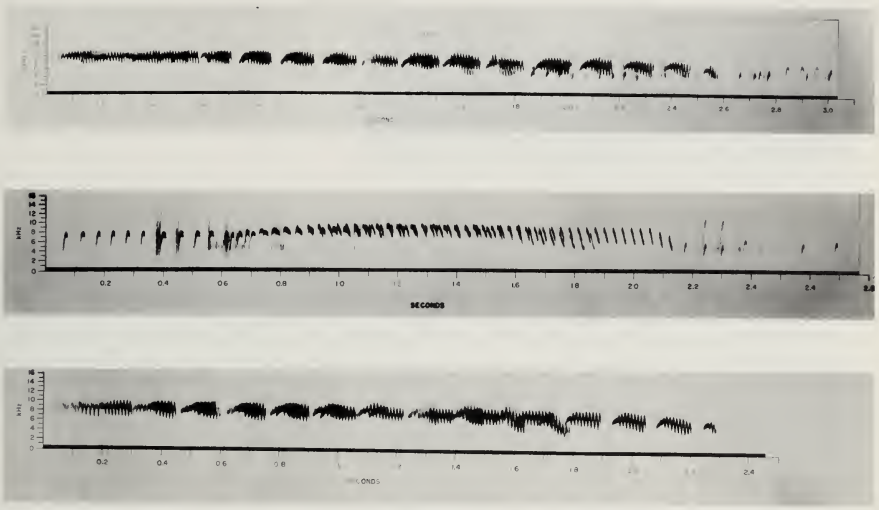


FIG. 6. Duet songs of *T. i. inexpectata*. Buzz duets (top and bottom); chatter duet (middle).

cording of song uttered its most rapid chips as it flew toward the tape recorder for the first time. The rate would decrease thereafter. Chips appear to be similar in function and used in similar contexts to similar callnotes found in many species of small passerine birds. Some stimulus, usually a predator or an intruding conspecific, is perceived that arouses the calling bird.

Song.—Torreornis pairs sing spectacularly intricate duets which are, to our knowledge, the only New World example of duets containing completely synchronized syllables. Duet syllables are either frequency modulated (buzz duets) (Fig. 6, bottom), pulse-like upslurs and/or downslurs (chatter duets) (Fig. 6, middle; Fig. 7, top). Duets may consist entirely of one or the other or contain both syllable types (Fig. 6, top, bottom). No difference in duet duration or syllable number per duet was found when comparing the two populations (Table 1).

All duets characteristically increase in amplitude, reaching a peak which is held for most of the duration, with a decrease toward the end. Often one or both birds change to chatter syllables at the end of a duet. The middle portion is 13.5 db greater in amplitude than the beginning or end, probably due to the complete synchronization that occurs in this portion. If these synchronous sounds are in phase the resulting amplification should permit the song to be broadcast over a larger area than if the synchronization was less precise. This cooperation in singing has not been previously

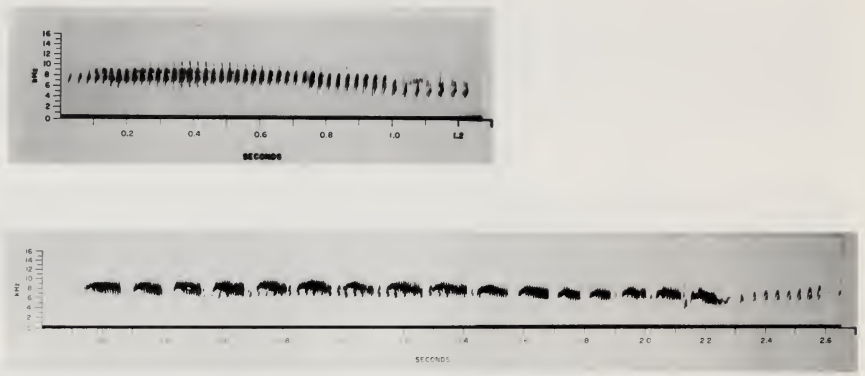


FIG. 7. Duet songs of *T. i. sigmani*. Combination buzz and chatter duet (bottom); chatter duet (top).

reported and may signify strong selection for mate cooperation in territorial defense.

We believe the male usually begins the song and his mate quickly joins in. Fig. 6 (top and bottom) illustrates the development of synchrony from the song beginning to about 0.6 sec. From then on, the rapid frequency modulated buzzes stay in perfect synchrony until one bird decreases its buzz frequency at 1.6 sec before changing from buzz to chatter syllables (Fig. 6, top) from 1.85 sec to the end of the song. Another duet from *T. i. inexpectata* (Fig. 6, bottom) included a frequency drop by one bird at 1.6 secs into the song. In this duet they lost the synchrony in buzz syllables, and neither pair member switched to chatter syllables. The chatter duet also exhibits syllable synchrony. In Fig. 7 (top), one bird begins with three notes, whereupon the second begins singing slightly higher frequency notes of the same shape as the initiator's; each lowers its note's frequency in synchrony after 0.75 sec into the song.

Each pair of *Torreornis* varies the structure of successive renditions of its song duets to such an extent that we could not distinguish pair-distinctive patterns. It was our impression that pairs of *T. i. inexpectata* sang proportionally more buzz duets, but the sample consisted of only four pairs. Both members used buzz syllables in two of 17 duets from *T. i. sigmani* (this sample of 10 pairs was ca 20% of the total population). In 11 of the 17, the male used buzz syllables while the female used chatter syllables as shown in Fig. 7 (bottom). However, we believe that chatter songs are more likely to occur as the first few songs sung in response to playback. For the *T. i. sigmani* study, we used a tape loop of *T. i. inexpectata* buzz duet for the stimulus and repeated it more frequently. For *T. i. inexpectata*, we used primarily playbacks of the buzz callnote to

Table 1

Composition of Duet Songs Comparing *T. i. inexpectata* and *T. i. sigmani*

Number of syllables[a]	Syllable type		Overall song length (sec)	Frequency range (kHz)
	buzz	chatter		
		T. i. inexpectata		
25	8	17	3.5	7–11
47	0	47	3.2	4–8
89	0	80	4.2	4–10
34	19	15	5.0	5–11
33	19	14	4.3	4–10
47	14	33	5.2	4–10
37	17	20	5.2	3–11
25	19	6	4.4	6.5–11
52	14	38	5.1	4–11
36	17	19	5.2	4–10
20	7	13	1.6	4–10
37	12	25	3.1	4–11
21	13	8	3.4	4-11
N = 13				
$\bar{x}$ = 38.7 ± 18.14			$\bar{x}$ = 4.1 ± 1.10	
		T. i. sigmani		
15	15	0	3.2	6–10
15	15	0	3.4	6.5–9.5
52	7	45	3.1	4–9.5
46	0	46	1.9	4–9.5
64	1	63	2.5	4–9.5
53	0	53	2.1	4–9
26	11	15	2.9	4–10
16	11	5	2.6	5–10
64	6	59	2.6	4–10
85	3	82	3.4	4–9
9	9	0	2.6	6–11
51	0	51	2.2	5–10
58	17	41	3.8	5–10
61	1	60	2.5	4–9
47	2	45	1.8	6–9
N = 15				
$\bar{x}$ = 44.1 ± 22.66			$\bar{x}$ = 2.7 ± 0.58	

[a] Neither population differed significantly in number of syllables or overall song length (*t*-test).

stimulate pairs, because we had nothing else. It is likely that the chatter duet is delivered by highly aroused birds, because these occurred immediately following playback in both populations and often followed aggression by one pair member toward the other just before they duetted.

We heard few natural duet songs. Even after a playback, duets were delivered only after a flight towards the source of the playback. The birds mostly looked for the "intruders" while perched high in vegetation.

DISCUSSION

T. inexpectata exhibits little difference in its four classes of sounds in two isolated populations. Distinct song differences have not developed despite the distance and long time period that separates the two populations. The only major difference appears in the modulation rate of the buzz callnote, *T. i. sigmani* having a faster rate than *T. i. inexpectata*. Buzz songs are more alike in the populations than chatter songs. *T. i. inexpectata* have chatter songs composed of three different elements that change from upslurred to downslurred during a song, whereas *T. i. sigmani* songs consist of upslurred elements. The extant populations are undoubtedly remnants, for fossils are known from caves outside the present range of the species (Pregill and Olson 1981). The current habitat differences (swamp vs arid scrub) may not differ in acoustic properties since the Zapata Swamp is nearly dry at certain times of the year, resulting in a habitat more like that of scrub grassland (Olson, pers. comm.).

Regalado (1981) describes three of the vocalizations of *T. i. varonai* from Cayo Coco as *tsik*, *chrii*, and song, which are similar to and correspond with our chip, buzz, and song. However, he mistakenly describes the song as a territorial duel between two males rather than a duet between a pair.

Like many other tropical passerines which have permanent territories and permanent pairbonds, duets appear to function in territorial defense (Farabaugh, in press). In addition, duets may evolve specifically to increase the effectiveness of territorial defense through reducing potential misguided aggression toward the pair member in the context of territorial intrusion. By coming in close proximity to one another, the pair members of monomorphic species, such as *Torreornis*, may avoid mistaking each other for an intruder and therefore more efficiently direct their aggression toward the real intruder. Synchrony may increase the duet's amplitude such that potential intruders are repelled at greater distances.

Given the emberizine heritage of *Torreornis*, it is remarkable that a greater difference in song was not found between the populations. Perhaps the fact that both sexes contribute to the complicated, synchronized duet, places constraints on divergence of the structure of the song. Perhaps individuals tending to diverge from the established song types are less apt to attract and maintain mates if potential mates are not able to effectively synchronize their songs with them.

The duet songs of *Torreornis* are similar in context of delivery to duet or chatter songs described for *Aimophila* sparrows (Wolf 1977) and to-

whees (*Pipilo* sp.) (Marshall 1964), but these also have male-only ("primary") songs which are lacking in *Torreornis*. The Rufous-crowned Sparrow (*Aimophila ruficeps*) chatter duet is structurally similar to a buzz-and-chatter-combination duet of *Torreornis* (see Wolf 1977:112). If *Torreornis* is closely related to *Aimophila*, as suggested by extensive morphological data (McKitrick, pers. comm.), then the loss of male-only song in *Torreornis* may have been coupled with a more complex development of the chatter or "pair reunion" duet found so extensively in *Aimophila*.

SUMMARY

The Zapata Finch (*Torreornis inexpectata*), endemic to Cuba, exists in three widely separated populations. Here we describe and compare the vocalizations of the Zapata Swamp population with the population living in a near-desert habitat 720 km to the east, near Baitiquiri. Adult *Torreornis* have a simple vocal repertoire of four sound types: chip, buzz, distress call, and song. Highly synchronous duet songs are used by pairs to defend territories throughout the year. The divergence in habitat and separation by distance have not resulted in major differences in the vocalizations of the two populations.

ACKNOWLEDGMENTS

The two expeditions permitting this study were superbly planned and logistically supported by the Instituto de Zoologia of the Cuban Academy of Sciences. Special gratitude is due to Dr. Fernando Gonzalez, Director of the Instituto de Zoologia, for his support and assistance during all phases of this research. Noel Gonzalez provided much help and field companionship during the expedition to study *T. i. sigmani*. In addition, Dr. Storrs Olson of the Smithsonian Institution happily verified the sexes of *T. i. sigmani* specimens and was an enthusiastic member of both expeditions. Dr. James F. Lynch, also of the Smithsonian, provided insight to the study of *T. i. sigmani*. We thank Storrs Olson and Luis Baptista for reviewing the manuscript. Sigrid Bruch and Judy Gradwohl graciously prepared the illustrations. Travel funds were provided by Fluid Research Funds from the Smithsonian Institution and from Friends of the National Zoo.

LITERATURE CITED

Baptista, L. F. 1976. Song dialects and demes in sedentary populations of White-crowned Sparrow (*Zonotrichia leucophrys nuttali*). Univ. Calif. Publ. Zool. 105:1–52.

Barbour, T. and J. L. Peters. 1927. Two more remarkable new birds from Cuba. Proc. New Eng. Zool. Club 9:95–97.

Farabaugh, S. M. In Press. The ecological and social significance of duetting. Chapt. 4. *in* Acoustic communication in birds (D. E. Kroodsma and E. H. Miller, eds.). Academic Press, New York, New York.

Marler, P. and M. Tamura. 1964. Culturally transmitted patterns of vocal behavior in sparrows. Science 1946:1483–1486.

Marshall, J. T. 1964. Voice in communication and relationships among Brown Towhees. Condor 66:345–356.

Morton, E. S. 1975. Ecological sources of selection on avian sounds. Am. Nat. 109:17–34.

Paynter, R. A. and R. W. Storer. 1970. Peters checklist of birds of the world. Vol. XIII. The Heffernan Press, Worcester, Massachusetts.

Pregill, G. K. and S. L. Olson. 1981. Zoogeography of West Indian vertebrates in relation to Pleistocene climatic cycles. Ann. Rev. Ecol. Syst. 12:75–98.

Regalado, P. R. 1981. El genero *Torreornis* (Aves, Fringillidae), descripcion de una nueva subespecie en Cayo Coco, Cuba. Centro Agricola 2:87–112.

Ripley, S. D. and G. E. Watson. 1956. Cuban bird notes. Postilla 26:1–6.

Spence, M. J. and B. L. Smith. 1961. A subspecies of *Torreornis inexpectata* from Cuba. Auk 78:95.

Wolf, L. L. 1977. Species relationships in the avian genus *Aimophila* Ornithol. Monogr. No. 23.

NATIONAL ZOOLOGICAL PARK, SMITHSON. INST., WASHINGTON, D.C. 20008 AND INSTITUTO DE ZOOLOGIA, ACAD. DE CIENCIAS DE CUBA, CALLE 212 ESQ. AVENIDA 19, RPTO. ATABEY, MUNICIPIO PLAYA, C. HABANA, CUBA.
ACCEPTED 18 Aug. 1982.

COLOR PLATE

The color plate Frontispiece of the Zapata Finch (*Torreornis inexpectata*) has been made possible by an endowment by George Miksch Sutton. Painting by John P. O'Neill.

FIRST ANNOUNCEMENT

XIX CONGRESSUS INTERNATIONALIS ORNITHOLOGICUS

At the XVIII International Ornithological Congress in Moscow the International Ornithological Committee accepted the invitation of the National Museum of Natural Sciences of Canada and of the Canadian ornithological community to hold the XIX Congress in Canada. The Congress will be held in Ottawa, Canada, from 22–29 June 1986. Dr. Prof. Klaus Immelmann (West Germany) was elected President of the Congress. Dr. Henri Ouellet (Canada) was designated as Secretary-General.

Details about the general and scientific programs, field excursions, and other activities during the Congress will be available later.

Those interested in participating in the Congress are urged to inform the Secretariat in order to obtain announcements and application forms. Correspondence should be addressed to The Secretary-General, Dr. Henri Ouellet, XIX Congressus Internationalis Ornithologicus, National Museum of Natural Sciences, National Museums of Canada, Ottawa, Ontario K1A 0M8, Canada.

Wilson Bull., 94(4), 1982, pp. 447–462

THE BEHAVIOR OF SCALE-BACKED ANTBIRDS

Edwin O. Willis

Among birds that regularly capture arthropods flushed by swarms of army ants in South American forests (Willis and Oniki 1978), one of the species lowest in peck orders is the Scale-backed Antbird (*Hylophylax poecilinota*). Here I report on the specialized behavior patterns that allow it to become one of the few antbirds that persist in moderately regular ant-following despite being excluded by three–five larger species.

STUDY AREAS AND METHODS

Between 1961 and 1979, I studied Scale-backed Antbirds in forests of Guyana (Nappi Creek, Bartica), Colombia (Mitú, Tres Esquinas, Umbria, Leticia), Ecuador (Zatzayacu, Limoncocha, Yaapi, Putuimi), Peru (Cashibococha, Andoas), and Brazil (Tangará da Serra, Benjamin Constant, Carauarí, Igapó-Açú, Borba, Coatá, Sucundurí, Maloquinha, Miriti-tuba, Palhão, Barreirinha, Serra do Navio, Belém, and at Km 60 and Reserva Ducke near Manaus). At Reserva Ducke (entrance at 2°55′S, 59°59′W) I color banded 28 birds during a study conducted from July 1973 to August 1974. Reserva Ducke is partly upland (80–120 m elev.) forest on yellow soil, partly sandy, valley forest (60–100 m elev.) with palms and streams, and partly second growth and plantations for forestry experiments (Willis 1977).

I observed Scale-backed Antbirds mainly from behind swarms of army ants (mostly *Eciton burchelli* at Manaus; in other regions, *Eciton rapax* and *Labidus praedator* were regularly attended as well). Occasionally I watched this antbird away from ants, but it is not easy to detect or follow even over ants. Mist-netted birds were weighed with Pesola scales, cloacal temperatures taken with a Schultheis thermometer, and voice recordings were made at a tape speed of 19 cm/sec with a Uher 4000 Report-S. I examined 1482 specimens in museums of Europe, the United States, and South America.

TAXONOMY

Scale-backed Antbirds range up to 1700 m elev. in tropical forests from eastern Colombia and the Guianas south to Bolivia and central Brazil. The mostly allopatric subspecies often differ strikingly in plumage. Hybrids between nominate *H. p. poecilinota* and a western subspecies (*H. p. duidae*) are known from a narrow zone at Mt. Duida in southern Venezuela (Zimmer 1934). Specimens of *H. p. duidae* and *H. p. poecilinota* are reported from Itacoatiara, near Reserva Ducke, causing Pinto (1978) to conclude that the two represent separate species. Near Manaus, the form *H. p. duidae* is usually reported only west of the Rio Negro, allopatric with nominate *H. p. poecilinota*. I found only nominate *H. p. poecilinota* at Reserva Ducke and Km 60, and wonder if specimens of *H. p. duidae* supposed to be from east of the Negro are mislabeled.

Scale-backed Antbirds do not look or behave like other species of the genus *Hylophylax*, which are plump and short-tailed. Instead, they re-

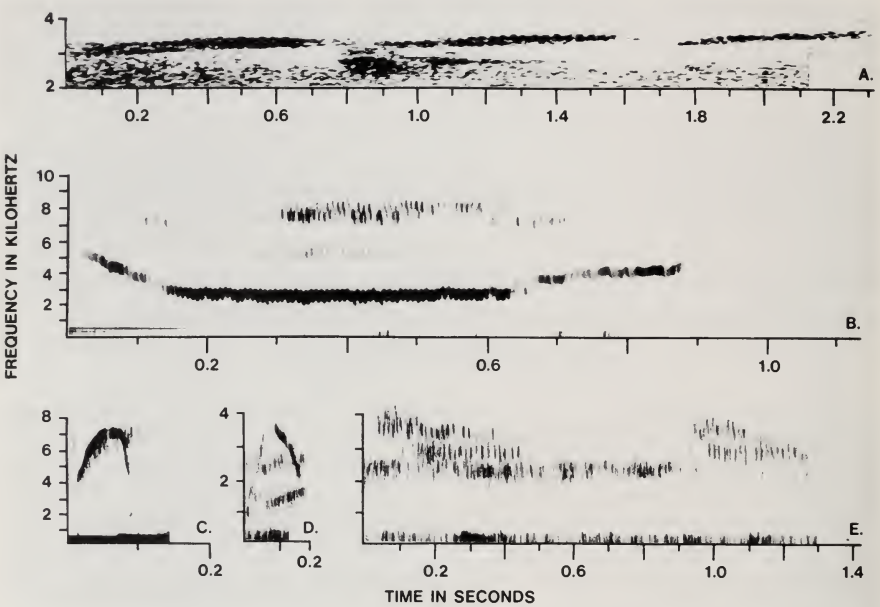


FIG. 1. Vocalizations of Scale-backed Antbirds. (A) "Song" of three notes, Manaus (narrow-band analysis); (B) "snarl" of female in the hand, Manaus; (C) "chip" of same bird; (D) "chirp" at Manaus; slightly inclined lines are background noise of other birds; (E) two faint *chirrs* at Manaus; band about 2.5 kHz is background noise.

semble slender swamp antbirds of the genus *Hypocnemoides*. The two genera should perhaps be combined. Birds of both genera resemble certain antwrens of the genus *Myrmotherula*: the Rufous-bellied Antwren (*M. guttata*) and the Plain-throated Antwren (*M. hauxwelli*) in morphology and behavior.

VOCALIZATIONS

The vocalizations of scale-backs are for the most part inconspicuous, in keeping with their generally unobtrusive behavior. Eleven types of sounds were detected.

Singing.—The song is a slow and inconspicuous series of a few faint, quavering whistles, which can be transliterated as *treeeeees*, *treeeees*, *treeees* (Fig. 1A). Whistles are successively shorter and higher in pitch; often the first few whistles are faint and buzzy. "Faintsongs" are faint versions or variants of the normal song, some of them double-noted (*bee tipee tipee*) as in Spotted Antbirds (*Hylophylax naevioides*). Often faintsongs alternate with series of chirping notes as a "serpentine song" when calling for young or for a mate.

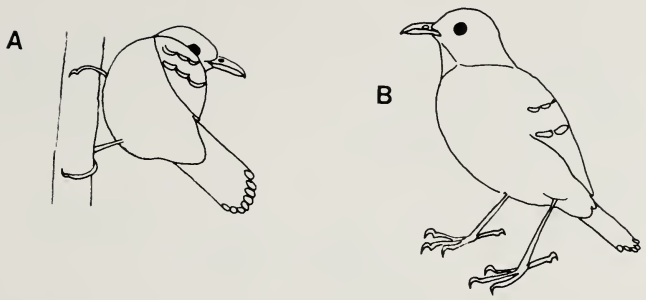


FIG. 2. Foraging postures of Scale-backed Antbirds, from field sketches. (A) Horizontal on vertical sapling, tail somewhat raised; (B) waiting on ground after prey ran under leaves.

Chirring.—A faint buzzy rattle, *chiiiiiiih*, is a common response to humans and other mammals (Fig. 1E).

Chipping.—Fleeing or fighting birds give loud *wreep* (Fig. 1C) notes (like an Acadian Flycatcher [*Empidonax virescens*]) north of the Amazon and south to the Ucayali in Peru (Cashibococha). Eastward, south of the Amazon, the call is sometimes double; and birds of the eastern subspecies (*H. p. nigrigula* and *H. p. vidua*) give a triple, high-pitched *sit-sit-sit* instead of the single-noted chip.

Growling.—During disputes, rough rising notes are commonly given two or three times: *zhaihh'eet zhaihheet*.

Snarling.—A faint *wrieeeh* sound is given toward a rival or when the bird is held in the hand (Fig. 1B).

Whimpering.—Subordinate birds give a series of three to four faint notes, *pseeh eeh eeh*.

Snapping.—The beak is snapped one to three times in supplantings.

Chirping.—Soft *peup* notes (Fig. 1D) are exchanged between mates, and parents and young, and other birds that are not fighting.

Chuttering.—A buzzy rustling, *ruh-uh-uh-uh-uh-uh-uh*, was noted at Miriti tuba (form *H. p. nigrigula*) when a male fed a female. A similar but high-pitched twitter was noted during feedings at Manaus.

Peepsinging.—Young birds (heard at Manaus, Cashibococha) give a loud, hawk-like *treeeeee treeeeeh treeeeh* at one pitch, without quavering; at times the sound is faint or includes as many as 10 notes.

Squeaking.—Young being fed give the usual avian *chiaahhh* noises.

ALARM BEHAVIOR

Scale-backed Antbirds are inconspicuous birds that stay on one perch for long periods of time or fly rapidly and stop abruptly; they probably escape predators in large part because of these foraging patterns. Specific

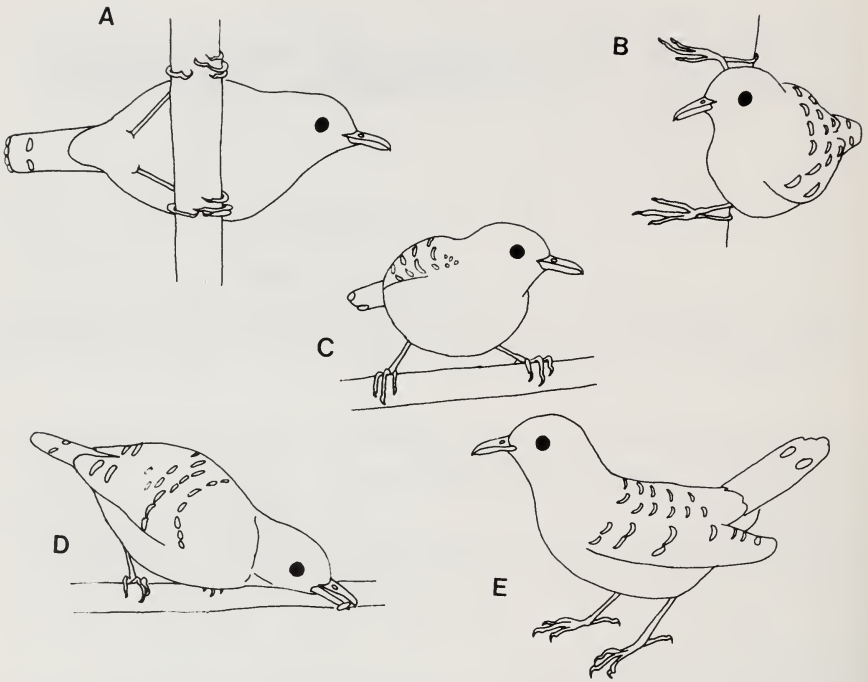


FIG. 3. Foraging and alarm postures of Scale-backed Antbirds. (A) Horizontal on vertical sapling. (B) Same, in front view, showing toe positions. (C) Crouched, freezing. (D) Head-down posture in eating prey. (E) Tail-up posture in hollow in leaf litter, waiting for prey.

responses to predators seem similar to those of related antbirds: freezing, fleeing, mobbing, struggling (in the hand), and habituation (tameness).

Freezing.—Normal foraging postures, straight and horizontal, like a study skin (Figs. 2, 3), involve so little movement (slight turning of the head or an occasional jump to a mirror-image pose) that they are essentially freezing. "Keening," the faint call of related antbirds during freezing, is not known from this species but may occur; it is a difficult call to detect in any species. One Scale-backed Antbird (Fig. 3C) crouched at the alarm chip of a Black-headed Antbird (*Percnostola rufifrons*).

Fleeing.—At the threat of close danger, Scale-backed Antbirds "chip" and flee abruptly, generally to dense cover in a treefall or to saplings growing up around the treefall. The chipping call seems to float in the dark undergrowth like ink behind a squid, and may be equally misleading to a predator. In the presence of moderate danger, such as a slowly moving human, the bird is likely to dart either a short distance away or behind a tree trunk and freeze. In response to less danger, such as a quiet observer

nearby, the bird sometimes flicks the tail upward slightly, to 20 or 30° above the line of the body, and slowly lets it drop to near the line of the body or slightly below. At times the tail remains upward for some time, as in aggressive behavior. The wings may flit outward slightly every few seconds, whether or not the bird is flicking its tail at long intervals. Sudden "about-faces" to mirror-image poses were recorded when a leaf fell and after minor movements of the observer. None of the movements are conspicuous. Chipping and fleeing was the response observed given to Barred Forest-Falcons (*Micrastur ruficollis*) twice, to alarm notes of Rufous-throated Antbirds (*Gymnopithys rufigula*) once, to release from the hand, to a downward glide of a Red-billed Woodcreeper (*Hylexetastes perrotti*), to a jump of a squirrel (*Sciurus*), and to a falling leaf. Chipping alone was recorded to the forest-falcons three times and twice during capture of insects at the unusual height of 5 m above the ground. Flight without chipping was recorded twice in response to my presence and once to the alarm note of a Red-necked Woodpecker (*Campephilus rubricollis*). Chipping caused alarm in other species at times (*G. rufigula* twice, Lunulated Antbird [*G. lunulata*] once, Bare-eyed Antbird [*Rhegmatorhina gymnops*] once, and White-chinned Woodcreeper [*Dendrocincla merula*] once).

Mobbing.—A "chirring" buzz, accompanied by slight upward movements of head and wings or tail, is a moderately frequent reaction to an observer or to *chirrs* of other antbirds. The faint sound is seldom repeated more than a few times before the bird resumes foraging or flees.

Struggling.—In the hand or mist net, this antbird occasionally "snarls" and struggles or pecks one's finger.

Taming.—Individuals watched more than a few minutes became quite tame, but were difficult to follow because of their normal elusive foraging movements to other parts of ant swarms. I often heard this antbird without seeing it despite several hours of observation. In part, this occurred because I watched the swarm center, where many species dominant to the scale-back occur, whereas it wandered peripheral to the center most of the time. Moreover, individuals are territorial and hence seldom saw me more than a few days as the ant colony passed through their areas; they could not become accustomed to me over several weeks as did birds that followed the ants wherever they and I wandered.

FORAGING BEHAVIOR

Scale-backs usually cling quietly and horizontally (Figs. 2, 3) to slender or thick saplings low (Table 1) in the understory of forest or second growth, dart quickly for any small prey that appears on the ground or on low foliage, and flee rapidly with prey unless it is swallowed immediately. Quiet, gray ghosts of the understory, scale-backs seem to appear and

TABLE 1
HEIGHTS OF PERCHES OF SCALE-BACKED ANTBIRDS

Height (m)	Over ants (%) N = 417	Before prey (%) N = 55
0 (ground)	1.6	—
0.1	4.8	20
0.2	13.7	24
0.3	13.7	15
0.4	13.4	11
0.5	13.4	7
0.6	10.1	7
0.7	6.2	—
0.8	5.5	7
0.9	1.0	—
1.0	3.4	—
2	11.0	5
3	1.0	2
4	1.2	2

disappear as if by magic; and they wander around the distant edges of ant swarms whenever large antbirds are present. All of these patterns could serve to reduce predation, but may also be adaptations to avoid being detected by larger competitors. Scale-backs occasionally forage in open undergrowth, where many of their larger and more conspicuous relatives show alarm behavior even when no predator is present. Use of thick saplings, otherwise occupied mainly by vertically-perching woodcreepers, differentiates the Scale-backed Antbird from other crosswise-perching antbirds. Its unusually long claws and toes, plus light body weight, allow it to perch crosswise on upright trunks over 4 cm diameter (Table 2). Other antbirds perch on large trunks mainly if the perch angle is under 45° from the horizontal, and slip or flutter even in brief attempts to perch on vertical thick trunks. Thirty-seven of 45 *H. poecilinota* perches over 4 cm diameter were over 45° angle, which is a ratio like that for perches of any diameter (318/383); one vertical perch was 35 cm diameter.

Scale-backs sometimes arrive at dawn at army ant colonies, chipping occasionally as they dart to perches nearby and then circle ahead of the ants. Others, following lines of ants past the observer to the swarm, arrive late in the day. At times, birds search and sing near areas where ants had been active the previous day. They regularly visit statary (Willis and Oniki 1978) colonies of ants, which are poorly attended by large antbirds because statary colonies do not swarm every day. These behavior patterns are characteristic of regular ant followers. I think that individual *H. poecili-*

TABLE 2
PERCH ANGLES AND DIAMETERS FOR SCALE-BACKED ANTBIRDS

Angle (°)	Over ants (%) N = 383	Before prey (%) N = 55	Diameter (cm)	Over ants (%) N = 357	Before prey (%) N = 52
0–20	10.2	13	0–1	33.6	46
21–40	5.7	7	2	38.4	37
41–60	4.2	6	3	13.7	6
61–80	9.9	14	4	5.0	8
81–100	69.5	58	5	2.2	—
101–120	0.5	2	6–15	6.4[a]	4
—	—	—	16–25	0.3	—
—	—	—	26–50	0.3	—

[a] 2.5% between 5.1 and 6.0 cm.

nota normally follow any army ants in their territories, but regularly forage away from ants when no ants are available. Wandering immatures probably follow ants even more regularly than do settled adults.

Birds waiting over ants or near them sit patiently up to 7 min, turning the head rarely. Now and then the closed tail twitches sidewise rapidly, or is lowered and then flicked upward. They pivot around their perches or reverse on them at times. Sidestepping crosswise down a perch before a prey attempt was recorded once. Movement of distant prey sometimes prompts a bird to fly to and watch from a perch above where the prey had hidden under the leaf litter. At long intervals there is a rapid flight to a more or less distant perch, occasionally to a perch near a large bird that is capturing prey. At Manaus, perches ahead of ants were used more (N = 291) than perches behind ants (N = 69); left (N = 158) and right (N = 148) ends of the swarms were used more than swarm centers (N = 16). They frequently (N = 41) used small branch raids, where there were few dominant antbird species. Treefalls (N = 14) and dense undergrowth (N = 12) were visited, as well as open understory (N = 6).

Over or near army ants, a quick sally to the ground and back to a perch is the most common foraging pattern (Table 3), as in most ant-following birds. Eight of 12 sallies were under 0.5 m from the perch; only two were 1.3–1.5 m off. Often the bird misses prey even on short sallies to the ground. Pecking an arthropod off the ground is fairly common, as is standing on the ground with tail up to toss leaves and peck any prey uncovered (Fig. 3E). Both grasping a leaf in the bill to toss it and nudging leaves aside with swipes of the bill were observed. Once a leaf-tossing bird pecked a tiny prey, then tossed more leaves and got a large prey. Occasionally a bird flies to the ground and waits before pecking prey or tossing leaves

TABLE 3
PLACES AND METHODS OF FORAGING: SCALE-BACKED ANTBIRDS OVER ANTS

Place	Method (% of N = 213)		
	Sally	Glean	Toss
Ground	69.0	7.0	3.8
Trunk, log	1.4	0.5	—
Liana	0.9	0.5	—
Stem	—	4.7	—
Foliage	7.0	1.4	—
Debris	0.5	—	—
Air	0.5	0.5	—
Unknown	2.3	—	—

(Fig. 2B) or even waits in a cavity among the litter. The scaled pattern may resemble leaf litter and conceal such waiting birds from predators or competitors. Pecking prey is also inconspicuous, involving sudden rotation downward and back from a vertical perch but then quiet eating (Fig. 3D) or waiting. Short sallies to leaves, lianas, trunks, or debris above the ground are conspicuous only briefly. Pecking at lianas sometimes involves rapid pecking at ants fleeing with larvae from a nest; larvae are eaten but worker ants tossed away.

Prey items recorded at Manaus included ant larvae, roaches, a spider, a centipede, a grasshopper, and a gecko. The largest items were about twice the length of the exposed bill, or about 3 cm long (Table 4). At other

TABLE 4
PREY AND PREY SIZES: SCALE-BACKED ANTBIRDS OVER ANTS

Prey	Number prey of given size (mm)			
	0–10	11–20	21–30	41–50
Spider	—	(1)[a]	1	—
Centipede	—	—	1	—
Roach	(1)	1	1 (2)	—
Katydid	—	—	1 (1)	—
Caterpillar	—	—	—	(1)
Ant, larva	10 (1)	1	—	—
winged	(2)	—	—	—
Gecko	—	—	1	—
Unknown	2 (2)	3 (3)	2	—

[a] Records at localities other than Manaus in parentheses.

localities, similar prey were recorded, plus several winged ants and a caterpillar about 4.5 cm long.

Scale-backs rarely flail or eat large prey near the capture sites. They normally flee several meters away, at times taking prey to the ground to dissect. Larger competitors, attracted by prey captures, often supplant birds that do stay after a conspicuous capture. Legs of large prey are often eaten first. Scale-backed Antbirds at times angle downward on a vertical perch to crush and shake small prey before eating.

In southeastern Colombia to Peru (Cashibococha), I often noted these antbirds moving as much as 8 m above the ground near ant probes up trees. In such wet or disturbed forests, there are enough vines and other foliage above the ground that the antbirds can use the zone, whereas at Manaus there is little vegetation 4–8 m up. Also, there are more competing low-foraging species of antbirds along much of the western edge of Amazonia, notably Lunulated Antbirds at Cashibococha.

Away from army ants, scale-backs wander near treefalls or dense undergrowth, taking perches like those used when above ants, then dropping to the ground for prey. Since I saw many individuals away from ants, even though they are hard to detect, I doubt that the species gets even half its food over ants.

COMPETITIVE BEHAVIOR

Most competitive interactions were intraspecific (Table 5), but this was mainly because this species avoids places where other antbirds congregate. Supplanting by larger birds mainly results in a chip of alarm and flight; no aggressive display was noted to other species. However, 18-g Scale-backed Antbirds should dominate 13-g Spot-backed Antbirds (*Hylophylax naevia*), which (unlike the very closely related 17-g Spotted Antbird west of the Andes) seldom follow ants persistently.

At localities away from Manaus, species recorded attacking Scale-backed Antbirds included Lunulated Antbirds (five supplantings, three displacings) at Cashibococha (Willis 1968), Sooty Antbirds (*Myrmeciza fortis*) (four supplantings), White-plumed Antbirds (*Pithys albifrons*) (two supplantings, one displacing), White-cheeked Antbird (*Gymnopithys leucaspis*), Salvin's Antbird (*G. salvini*), White-breasted Antbird (*Rhegmatorhina hoffmannsi*), and the Crested Antbird (*R. cristata*) (one supplanting each). Twelve intraspecific supplantings were recorded in the same sets of observations. The rather frequent supplantings by Lunulated Antbirds are interesting, because females of that species have a scaled pattern above. Both *G. lunulata* and *G. salvini* forage somewhat like *H. poecilinota*.

Intraspecific competitive behavior is based on resident pairs and fairly strict territoriality. Wandering immatures and other birds are chased about

Table 5
Competitive Interactions of Scale-backed Antbirds and Other Birds at Manaus

Species	Supplant	Displace	Return	Ignore
Hylophylax poecilinota	67	—	—	—
Gymnopithys rufigula	/3[a]	/5	1	—
Pithys albifrons	/4	/3	—	—
Percnostola rufifrons	/1	/1	—	—
Dendrocincla merula	—	/1	1	—
D. fuliginosa (Plain-brown Woodcreeper)	/1	—	—	—
Hylexetastes perrotti	—	/1	—	—
Myrmeciza ferruginea (Ferruginous-backed Antbird)	—	—	—	1
Conopophaga aurita (Chestnut-belted Gnateater)	—	/1	—	—
Attila spadiceus (Bright-rumped Attila)	—	/1	—	—

[a] Records below diagonal are of attacks on *H. poecilinota* by another species.

and threatened repeatedly. Chases often bring chipping notes, usually from the aggressor, as a subordinate bird whimpers or pivots backward and forward indecisively before fleeing. Other than whimpering, submissive behavior is not conspicuous: the closed tail is lowered, the head feathers are slightly ruffed, and the bird flees rapidly from one perch to another 10–50 m apart. Young or wandering subordinate birds commonly circle about an ant swarm despite chases, but trespassing neighbors are likely to go to a different swarm fork or to leave.

Aggressive behavior is well developed, but inconspicuous and hard to follow. The closed tail is often raised to 30° above the line of the body, showing the pale undertail coverts (Fig. 4A). At times, an upwardly pointed bill displays the pale throat of some races or a dark throat in others. The bird sometimes snarls before flying at an opponent, or snaps its bill as it chases another. Strong threats between evenly matched birds commonly include rather loud "growls." The sleeked head is jerked up with each growl note (Fig. 4B). Some races have white bases to some dorsal feathers, and these bases are probably displayed by back-fluffing in threat display. I did not see strong forms of threat, for it was difficult to follow birds as they moved rapidly during disputes; fluffed-bodied or spread-winged types of threat are likely to occur as in most related species.

Songs seem faint, and are mostly used between mates, but often follow or precede territorial disputes. I doubt that any but the loudest songs are audible across a normal territory, but the birds may detect their own

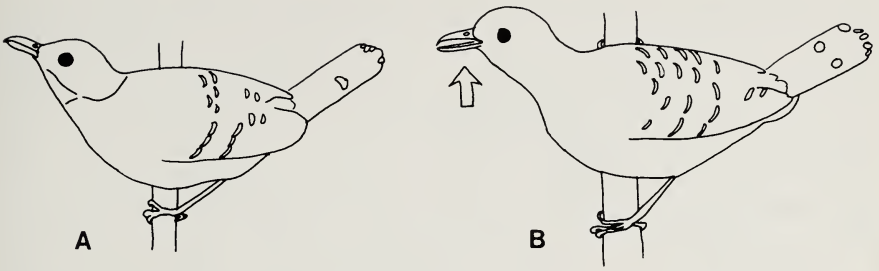


FIG. 4. Aggressive posture of Scale-backed Antbirds. (A) Head-up tail-up posture. (B) Head jerking during snarling.

sounds better than I did. Songs are as rare at dawn as during the day throughout the year.

REPRODUCTIVE BEHAVIOR

Pairs of Scale-backed Antbirds wander separately around swarms of ants if other dominant birds are present, but associate loosely away from competitors or away from ants. Often one does not see both birds at first, but occasional chirping or faintsong exchanges show that the mate is somewhere near. (One male kept chirping and singing to a female that took me 1 h to see.) Distant mates give fairly loud songs and move together. One female supplanted her mate.

As in most antbirds, males feed females. The male, prey in bill, faint-sings or serpentine-sings until the female flies up or responds, then flies to her and gives her the food. Usually there is a *chuttering* sound. The female normally flees with prey, dissecting it on the ground at times; the male chirps or faint-sings and returns to foraging. Occasionally the female stays near the male and, her head down, chews the prey. Presumably, as in related antbirds, copulation occasionally follows the last type of feeding.

One male at Mirituba serpentine-sang between the buttresses of a small tree, pecking at the ground and flicking his tail as if showing a nest-site to his nearby mate, after feeding her several times. (Such nest-showing behavior by males occurs in several antbird species [Willis 1967, 1972]). He ignored a nearby seedling. Pinto (1953) recorded a ground nest and two eggs, found by C. Estevão next to a tree trunk at Orá near Belém on 2 December 1924; the male was incubating. Snethlage (1935) found a nest in a low stub that contained two reddish-violet eggs with dark streaks and flecks.

Several well-grown young birds were banded out of the nest at Manaus between early November and early December 1973 (two broods) and from early June–late July 1974 (four broods). When separated from their par-

ents, the fledglings have "peep-singing" calls that are often very loud, so much so that I thought them calls of some hawk at first. One such young circled about when I tried to chase it, staying near the dense undergrowth in which the parent had presumably left it. Young following their parents peep faintly, like crickets. The male cares for one young and the female for the other whenever there are two young. One parent sometimes supplants the young of the other. A parent with food utters chirps or serpentine-songs and feeds the squeaking young. Young follow adults for at least 1 month (3 December–1 January in one case) and probably longer. All banded young had tails as long as those of adults and thus (judging from normal growth rates in antbirds) were at least 2 weeks out of the nest when discovered, so that care of fledglings lasts at least 6 weeks.

Young never stayed with their parents after independence. Banded young males wandered, often following army ants, in limited areas. One settled and found a mate in the same general area where banded (male GYRO, Fig. 5).

Nesting apparently occurs throughout the year except in central Venezuela (see below), as specimens of young males in similar stages of molt have been taken throughout the year in most regions. From the limited data, it seems possible that there are two nesting seasons a year at Manaus, as is characteristic of Black-headed Antbirds there (Willis, in press).

MOLT AND MAINTENANCE BEHAVIOR

Young change from a dusky head and body plumage into a plumage like that of the adult female while still with their parents. The crown and chest regions of the brownish-dusky young birds tend to be especially dark, and the belly is usually downy gray. The tail feathers have white tips and black subterminal bands as in the adult female (as do some mantle feathers in subspecies in which the female is scaled above). Museum specimens in juvenal plumage include two that have short tails (a female from Borba, 15 February 1930, AMNH 279540; a male from Tome-Açú, 29 September 1965, Museu Goeldi 26176), three that are dark with little evidence of molt to the female plumage (unsexed birds from Peixe-Boi, 16 May 1908, Museu Goeldi 5797 and 9 May 1910, Munich 10–1138; a male from Tucunaré, 12 December 1908, Frankfurt 38–815), and three that are molting into the orange head feathers of the female plumage (males from São Paulo de Olivença, 27 February and 1 March 1923, Carnegie 95594 and 95626; male from Mt. Duida, 1 April 1913, AMNH 120708). Young birds at Manaus seemed more scaled above than the adult female, but this character needs to be checked.

An unknown number of months after independence, young males change to the plumage of the adult male by an obvious molt that includes the wing

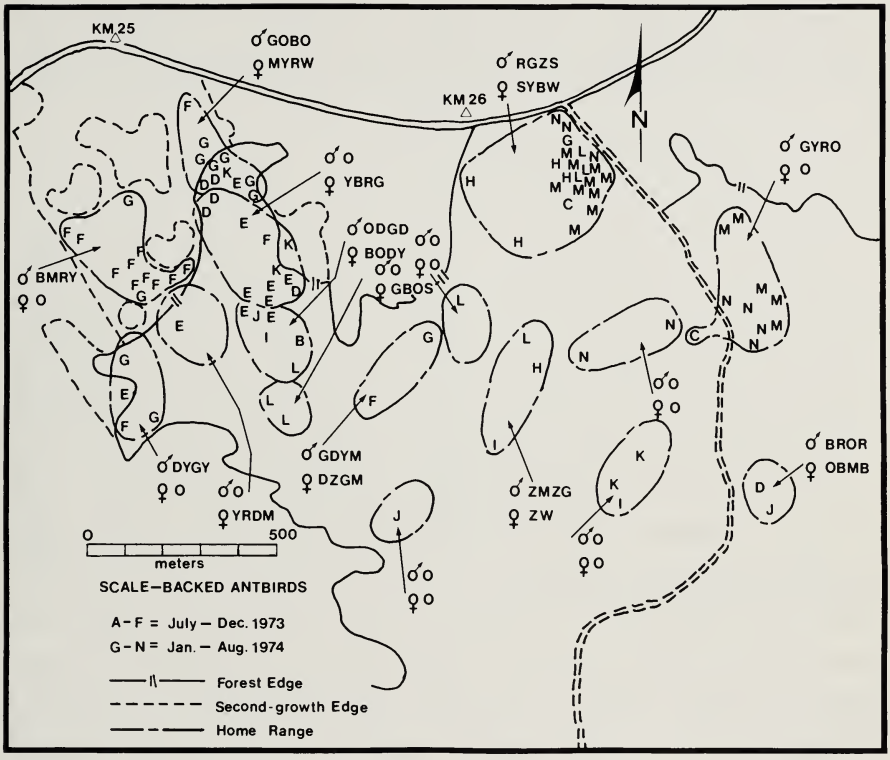


FIG. 5. Ranges of Scale-backed Antbirds near the entrance of Reserva Ducke in 1973–74. Banded birds have four-letter designations, unbanded birds are marked "O."

and tail feathers. Scattered blue-gray feathers appear on chest and head, then white-tipped ones replace rust-tipped or brown ones across the back and wings. Center tail feathers and new inner primaries are only replaced well after the start of body molt, so that the young male is very mottled by the time primary number three or four is being replaced. A few brown or orange feathers of the immature plumage sometimes remain after the outer remiges and rectrices have been replaced, however.

Unfortunately, I was unable to follow young birds to determine if young females undergo such molt or at what age the young males undergo molt. One young male, independent and in female plumage 15 September–28 October, was in full male plumage 9 July. Another, with scattered blue feathers and inner tertials 10 September, was nearly in adult plumage 25 November. Probably he started molt in late August and finished in December, 4 months later. Venezuelan specimens of young males in early molt were taken from August to February and ones in late molt from

January to May, suggesting that about 4–5 months are required for wing molt. Venezuelan birds probably nest in the rainy season, March to October, and young males are in adult plumage by the next nesting season. If so, they would keep the female plumage until about 6–8 months out of the nest and finish molt by the time they are 12 months out of the nest. Black-headed Antbirds, another antbird where young males are like females, have that type of molt schedule at Manaus (Willis, in press).

At Manaus, several adults were in molt between August and January. One banded adult female, ending molt (primaries 9 and 10 in molt) in early October, was at nearly the same stage of molt (primary 10 in molt) in mid-January. She then had young out of the nest by 15 July, and had not started molt by 27 July. Unless molt is rapid, taking fewer than the 4 months common among tropical antbirds, she must have arrested her molt in late 1973 (perhaps to attempt a nesting?) and delayed her molt in 1974 until the young were relatively independent. No birds with dependent young out of the nest were in molt, suggesting that molt does not overlap nesting or care of fledglings (unless arrested molt does so). Specimens in or not in molt date from all months of the year; there is no season of molt evident even in Venezuelan specimens.

Preening birds often sit and fluff out their body feathers; dense cover away from the ants is preferred. A few records (7–9) range to 0.7 m and up, 5 cm diameter, and 35° perch angle, suggesting that high and vertical perches are not used for preening. The head is scratched over the wing or wiped on the side of the perch. A full left stretch (wing, leg, and half the tail) interrupted one preening session.

SPATIAL BEHAVIOR

I have seen Scale-backed Antbirds mainly in the shady understory of upland forests and nearby tall second growth, or in the dense rows of forest plantations. At Belém, they usually avoided flooded forests (várzeas), but at Maloquinha and Carauarí I found them in várzea edges. They forage in relatively open understory, near dense cover.

Ranges of pairs overlapped little, although birds sometimes wandered undetected on each others' areas or followed large ant swarms into each others' areas (Fig. 5). Normally only one bird or pair, rarely a pair and a wandering bird, or one or two young, followed a given ant colony (Table 6).

Two territories in tall second growth had centers about 300 m apart, but several territories in the nearby forest had centers 200–300 m apart. There were 13 or 14 territories in the mature-forested northwestern 106 ha of the study area at Manaus, or about 8.2 ha per pair. Within the 106 ha there were at least 10 wandering immatures. Based on a mean body

TABLE 6

SWARMS OF *ECITON BURCHELLI* (FORMICIDAE) WITH GIVEN NUMBERS OF SCALE-BACKED ANTBIRDS

Month	No. of swarms with given no. of birds				
	0	1	2	3	4
July 1973	13	4	2	—	—
August	41	10	6	—	—
September	60	19	1	—	—
October	33	14	12	—	—
November	50	17	10	2	1
December	31	15	12	2	4
January 1974	40	23	8	—	—
February	37	18	3	—	—
March	37	11	2	—	—
April	53	12	3	—	—
May	36	20	3	1	—
June	30	16	9	1	1
July	24	10	17	1	—
August	15	8	10	1	—

weight of 17.9 g (15.7–19.4, N = 21) per individual at Manaus, biomass would have been approximately 4.6 g/ha for residents and 1.7 g/ha for wandering birds, or a total of 6.3 g/ha. Some of the forested area seemed not to be used by Scale-backed Antbirds, although more observation perhaps would have shown use; if some of the forest was unsuitable, density in suitable forest would have been higher than calculated above.

DISCUSSION

The foraging style of Scale-backed Antbirds differs from the styles of other ant-following birds, adding yet more diversity to that already noted among subordinate species over ants (Willis and Oniki 1978). This species is the lowest bird in ant-following hierarchies in most Amazonian localities; only species that follow ants casually are subordinate to it. The perching methods of Scale-backed Antbirds (quiet waiting on vertical perches at some distance from ants) and their silent and inconspicuous movements must help them to forage where most competitors are larger and more dominant.

Molt and breeding probably alternate and occupy much of the year, a situation permitted by the relatively nonseasonal climates of equatorial forests. It is likely that populations in central Venezuela may breed mainly in the northern summer and ones from Mato Grosso mainly in the southern

summer, but most birds probably breed two or more times a year. Two breeding seasons, one in the southern spring and one in the northern spring to summer, are suspected for Black-headed and Scale-backed antbirds at Manaus.

SUMMARY

Scale-backed Antbirds (*Hylophylax poecilinota*) are 18-g birds that follow swarms of army ants for flushed prey near the ground in South American lowland forests. They evade larger ant-following species partly by being quiet and inconspicuous or immobile for long periods; they also cling to larger vertical perches in more open understory than do large antbirds; and they wander at the margins of ant swarms or leave the ants when many large birds are present. Horizontal postures and long toes allow them to cling to large trunks. At Manaus, Brazil, pairs occupy territories of about 8.2 ha and chase trespassing immatures or neighbors. Dusky young remain with parents at least 6 weeks after leaving the nest, while undergoing body molt to a plumage like that of the adult female. Young males later molt to a plumage like that of the adult male. Breeding and molt occur all year, but are not known to overlap in an individual bird. There may be two breeding seasons per year at Manaus.

ACKNOWLEDGMENTS

Grant GB-32921 from the National Science Foundation supported studies at Manaus and Belém, while earlier studies were supported by Frank M. Chapman fellowships from the American Museum of Natural History and a Woodrow Wilson Foundation scholarship. I appreciate the help of Douglas Wechsler and of the staff of the Instituto Nacional de Pesquisas da Amazonia at Manaus. Yoshika Oniki helped in many ways.

LITERATURE CITED

Pinto, O. 1953. Sobre a coleção Carlos Estevão de peles, ninhos e ovos de Belém (Pará). Pap. Avuls. Dept. Zool., S. Paulo 11:113–224.

———. 1978. Novo catálogo das aves do Brasil. Primeira parte. Empresa Gráfica da Revista dos Tribunais. São Paulo.

Snethlage, E. 1935. Beitrage zur Fortpflanzungsbiologie brasilianischer Vögel. J. Orn. 83:532–562.

Willis, E. O. 1967. The behavior of Bicolored Antbirds. Univ. Calif. Publs. Zool. 79:1–132.

———. 1968. Studies of the behavior of Lunulated and Salvin's antbirds. Condor 70:128–148.

———. 1972. The behavior of Spotted Antbirds. Ornithol. Monogr. No. 10.

———. 1977. Lista preliminar das aves da parte noroeste e áreas vizinhas da Reserva Ducke. Amazonas. Brasil. Rev. Brasil. Biol. 37:585–601.

——— and Y. Oniki. 1978. Birds and army ants. Ann. Rev. Ecol. Syst. 9:243–263.

Zimmer, J. T. 1934. Studies of Peruvian birds. XII. Notes on *Hylophylax*, *Myrmothera*, and *Grallaria*. Am. Mus. Novit. 703:1–21.

DEPT. BIOLOGY, UNIV. MIAMI, CORAL GABLES, FLORIDA 33124. (PRESENT ADDRESS: DEPT. ZOOL., UNESP-RIO CLARO, CAIXA POSTAL 178, 13500 RIO CLARO, S.P., BRAZIL.) ACCEPTED 2 JAN. 1982.

Wilson Bull., 94(4), 1982, pp. 463–476

CENSUSES AND BREEDING OBSERVATIONS OF THE BIRDS ON KOHALA MOUNTAIN, HAWAII

Charles van Riper, III

The Kohala Mountain Forest remains one of the least known areas in the Hawaiian archipelago. A wide variety of avian species was found there during the late 1800's (Wilson and Evans 1890–1899, Rothschild 1893–1900). Palmer (p. 58 *in* Rothschild 1893–1900) collected one of the few specimens of the Ula-ai-hawane (*Ciridops anna*) and Perkins (1901) reported this forest to be one of the last strongholds of the Ou (*Psittirostra psittacea*) on Hawaii. Since 1900 there has been little ornithological work done in this region; Pratt (1967) recorded five native bird species in the southernmost part of the forest, but Donaghho (1971) failed to find any native birds in an expedition along the northern slope of the mountain. Berger (1975) and van Riper (1973, 1974, 1976, 1978a) reported on open-habitat birds, most of which were introduced species.

Because so little suitable habitat remains in the islands for Hawaii's endemic birds, it is imperative to document extant forest areas which contain threatened or endangered species. From 1969–1972 I conducted censuses and recorded the breeding behavior of birds in Kohala Mountain Forest, attempting to (1) define composition of the present avifauna, (2) measure uniformity of species composition throughout the forest, (3) quantify relative population numbers of each species, and (4) delimit aspects of the breeding seasons.

METHODS

Study area.—The Kohala Mountain Forest is a mesic ecosystem with a mixed canopy of ʻōhiʻa (*Metrosideros collina*) and ʻōlapa (*Cheirodendron trigynum*) trees, underlain by tree ferns (*Cibotium* spp.) and other subcanopy tree species of which *Pelea* ssp. are the most common. The vegetation of this area is most similar to that of East and West Maui, being different from any other forest on the island of Hawaii (Rock 1913). The paucity of fieldwork in this area has been largely due to the rugged terrain. The forest is bounded on two sides by the precipitous canyons of Honokane on the west and Waipio Valley on the east, and by sheer sea cliffs to the north. Only limited access is available from the south through private ranch lands.

The principal study area was a 0.25-km² quadrat at 1100 m elev. between Puu Laelae and Kohakohau Gulch (Fig. 1). Comparative census locations were the Kehena Ditch Trail, Eke, and Kawainui Stream area. In pasture areas surrounding the forest, numerous incidental sightings were noted.

Techniques.—Breeding observations were made throughout the 3 years of the study. During 1971 and 1972, 222 h were spent censusing during 47 daily-count periods. I made most observations during the peak breeding season (February to May); however, censuses were also undertaken in an early, late, and a nonbreeding period (January, July, and November,

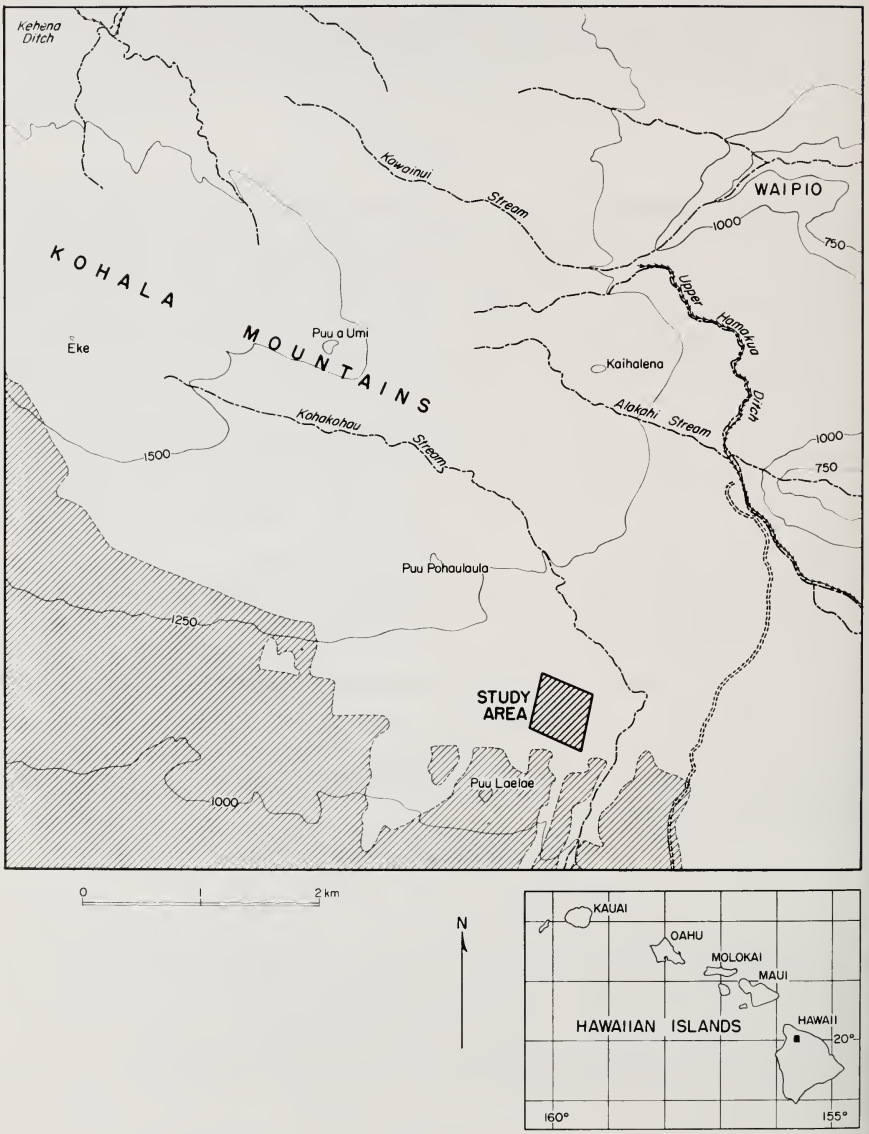


FIG. 1. Map of a portion of Kohala Mountain, Hawaii, showing the study area (dark hashing) and locations where comparative censuses were conducted. Elevation contours are in meters, double dashed lines are jeep roads, and light hashing denotes pasture land adjacent to the forest.

respectively). Strip transect counts were conducted (Emlen 1971); however, unlike Emlen's technique, the perpendicular distance of the bird from the observer's path of travel was not recorded.

A total of 38 daily counts was made in the principal study area in which 178 h were spent censusing. The counts were from 07:00 through 12:00 and conducted at a slow uninterrupted pace. Count periods averaged 4.7 h, but were of unequal length because of variable weather conditions. All birds were recorded as either an aural or visual detection, and age and sex were noted whenever possible. In order to minimize double registrations, the time, location, and direction of flight were recorded. No "squeaking" or other sounds were used to lure birds.

On alternate months during the peak breeding season, comparative counts were conducted in habitat of the Kohala Mountain Forest which was similar to that of the principal study area. A total of 44 h was spent during 9 days of comparative censusing, three each at the Kehena Ditch, Eke, and Kawainui Stream. These counts were conducted on the day following a census in the principal study area, under similar weather conditions, and during the same time period as the previous day's census.

The numbers of each species encountered per hour of censusing were used to describe abundance levels (Rotenberry and Wiens 1976). These data were then used to define:

$$\text{relative abundance of species } i = N_i/A$$

where N_i = total number of individuals of the ith species recorded and A = total number of the most abundant species; and

$$\text{frequency of species } i = S_i/S_t$$

where S_i = number of count periods in which the ith species was observed and S_t = total number of counts; and

$$\text{incidence of species } i = N_i/S_i.$$

All statistical analyses were computed on a Burroughs 6700 using SPSS programs (Nie et al. 1975). Where data were not normally distributed, transformations were used before application of statistical tests. The level of statistical significance was considered to be $P \leq 0.05$.

RESULTS AND DISCUSSION

Species distribution and abundance.—A total of 13 bird species was recorded during censuses in the Kohala Mountain Forest, while 16 other species were noted during incidental observations on the mountain. Native species predominated in the forest area (Table 1), while introduced species were more common in the pasture land and introduced forests at lower elevations.

Native species.—The native raptors preferred open pasture habitat to that of the closed-canopy forest. Numerous incidental sightings of the Hawaiian Hawk and the Short-eared Owl were made outside of the forest. The hawk was most frequently observed soaring over the deep valleys on the northern and northeastern edges of the forest while the owl was most common over pasture lands. Because of releases by the Hawaii Division

TABLE 1

BIRDS RECORDED IN THE KOHALA MOUNTAIN FOREST DURING 47 COUNT PERIODS FROM 1970–1972

Species	No. counts in which species were observed	Total birds recorded		Relative abundance	Species frequency	Species incidence
		No. aural	No. visual			
Hawaiian Duck (=koloa) (*Anas wyvilliana*)	2	—	4	0.004	0.04	2.00
Hawaiian Hawk (='io) (*Buteo solitarius*)	2	—	2	0.002	0.04	1.00
Short-eared Owl (=pueo) (*Asio flammeus*)	2	—	2	0.002	0.04	1.00
Red-billed Leiothrix* (*Leiothrix lutea*)	34	191	23	0.230	0.72	6.29
Melodious Laughing-thrush* (*Garrulax canorus*)	1	1	—	0.001	0.02	1.00
Elepaio (*Chasiempis sandwichensis*)	44	160	172	0.360	0.94	7.55
Japanese White-eye* (*Zosterops japonicus*)	42	613	229	0.910	0.89	20.05
House Finch* (*Carpodacus mexicanus*)	6	22	11	0.040	0.13	5.50
Common Amakihi (*Hemignathus virens*)	46	421	280	0.760	0.98	15.24
Hawaii Creeper (*Oreomystis mana*)	7	1	10	0.010	0.15	1.57
Nukupuu (*Hemignathus lucidus*)	1	—	1	0.001	0.02	1.00
Apapane (*Himatione sanguinea*)	45	800	323	1.000	0.96	24.96
Iiwi (*Vestiaria coccinea*)	33	188	93	0.300	0.70	8.52

* Denotes introduced species.

of Fish and Game, the Hawaiian Duck has recently been returned to the Kohala Mountain Forest. The greatest concentration of Hawaiian Ducks is presently in the Kahua Ranch (the principal Fish and Game release site), scattered throughout the smaller cattle watering holes up to the boundary of the forest near the Kehena Ditch. One pair was observed in

the Hamakua Ditch during incidental sighting periods throughout 1971, but no young were seen.

The most frequently observed native birds during censusing were passerines, of which the endemic Drepanidinae were the most common. The Apapane and Amakihi were found throughout most of the forest whereas the Iiwi was much more localized, being found only where extensive stands of larger 'ōhi'a occurred. The endangered Hawaii Creeper was observed most often in the forest between Puu Eke and the Kehena Ditch Trail, being quite rare to absent in other areas of the forest. The Nukupuu, which heretofore has not been reported from the island of Hawaii, was observed during one count period. The single observation was made on 29 June 1971, and was of a very bright yellow male fluttering in front of and probing into the blossoms of 'ōhi'a trees. Because of the open and low stature of the forest I was able to observe this bird at close range for an extended time period. At first I believed the bird to be an Akiapolaau (*Hemignathus munroi*), but it lacked the straight, robust lower mandible characteristic of that species. Instead, the lower mandible fit into the curve of the upper portion, and was about one-half as long. The bird was also seen by G. Haines, and in the following week we compared descriptions in our field notes with specimens at the Bishop Museum in Honolulu. The bird we observed most closely resembled the Maui subspecies of the Nukupuu, in size, color, and appearance of the bill.

It is possible that the bird was a straggler from Maui. However, because of the extreme rarity of the Maui race, this origin seems unlikely. After more than 50 years of no records, the Nukupuu was "rediscovered" on Maui in 1967 (Banko 1968). Even though much fieldwork has been done on that island since then, very few additional sightings of this bird have been made (Conant 1981a).

The bird could also represent a Hawaiian population of the Nukupuu. There is in fact little basis for the assumption that the Akiapolaau replaced the Nukupuu on Hawaii, seeing that the former rarely if ever takes nectar and the latter does so quite frequently (Perkins 1903). The Kohala Mountain Forest, in age as well as species composition, is more similar to that of Maui than to any other forest of Hawaii (Rock 1913). Therefore, the Kohala Mountain Forest would be more favorable to Nukupuu occupancy than any other area on the island of Hawaii.

Introduced species.—Of the introduced species, only the Japanese White-eye and Red-billed Leiothrix were consistently found within the Kohala Mountain Forest during counts (Table 1). The House Finch preferred open, disturbed pasture over the more dense forest habitat (see also van Riper 1976). Only one Melodious Laughing-thrush (*Garrulax canorus*) was re-

TABLE 2

MONTHLY RELATIVE ABUNDANCE OF BIRD SPECIES AS DETERMINED FROM 47 COUNT PERIODS CONDUCTED FROM 1970–1972 IN THE KOHALA MOUNTAIN FOREST, HAWAII

Species	Month						
	January (172.5)[a]	February (150.5)	March (375.5)	April (79.0)	May (215.0)	July (101.0)	November (21.0)
Amakihi	1.00	0.71	0.52	0.37	0.34	0.31	0.17
(701)[b]	(228)[c]	(214)	(157)	(31)	(59)	(8)	(4)
Apapane	0.75	1.00	0.53	1.00	0.96	0.65	1.00
(1123)	(170)	(302)	(162)	(83)	(166)	(17)	(23)
Elepaio	0.19	0.22	0.36	0.28	0.35	1.00	0.17
(332)	(44)	(66)	(109)	(23)	(60)	(26)	(4)
Iiwi	0.13	0.36	0.29	0.23	0.18	0.08	—
(281)	(30)	(110)	(89)	(19)	(31)	(2)	(0)
Red-billed Leiothrix	0.06	0.07	0.26	0.42	0.25	0.77	0.13
(214)	(14)	(21)	(78)	(35)	(43)	(20)	(3)
Japanese White-eye	0.37	0.67	1.00	0.75	1.00	0.58	—
(842)	(85)	(202)	(304)	(62)	(173)	(15)	(0)

[a] Numbers in parenthesis = total census hours.
[b] Numbers in parenthesis = total birds counted.
[c] Numbers in parenthesis = total birds counted that month.

corded during the two years of this study; but, the U.S. Fish and Wildlife Service has just completed a census of the area and has found that this species has greatly increased in numbers in the 10-year period between the two census efforts (J. M. Scott, pers. comm.).

A number of introduced species were noted on the periphery of the forest but not recorded during count periods. Nests of the Northern Cardinal (*Cardinalis cardinalis*) and Nutmeg Mannikin (*Lonchura punctulata*) were found on the forest edge, and single individuals were observed deeper in the forest. Eurasian Skylarks (*Alauda arvensis*) nested and foraged only in pastures outside of the forest. The House Sparrow (*Passer domesticus*) and Common Mynah (*Acridotheres tristis*) were found only near human habitations, while the Saffron Finch (*Sicalis flaveola*) and Warbling Silverbill (*Lonchura malabarica*) were occasionally observed at lower elevations in the introduced forests. The Rock Dove (*Columba livia*), Spotted Dove (*Streptopelia chinensis*), Zebra Dove (*Geopelia striata*), and Barn Owl (*Tyto alba*) were all recorded at elevations well below the forest boundary. Numerous game species released by the Hawaii Division of Fish and Game have become established in the pasture lands adjacent to the Kohala Mountain Forest and were recorded during incidental observations

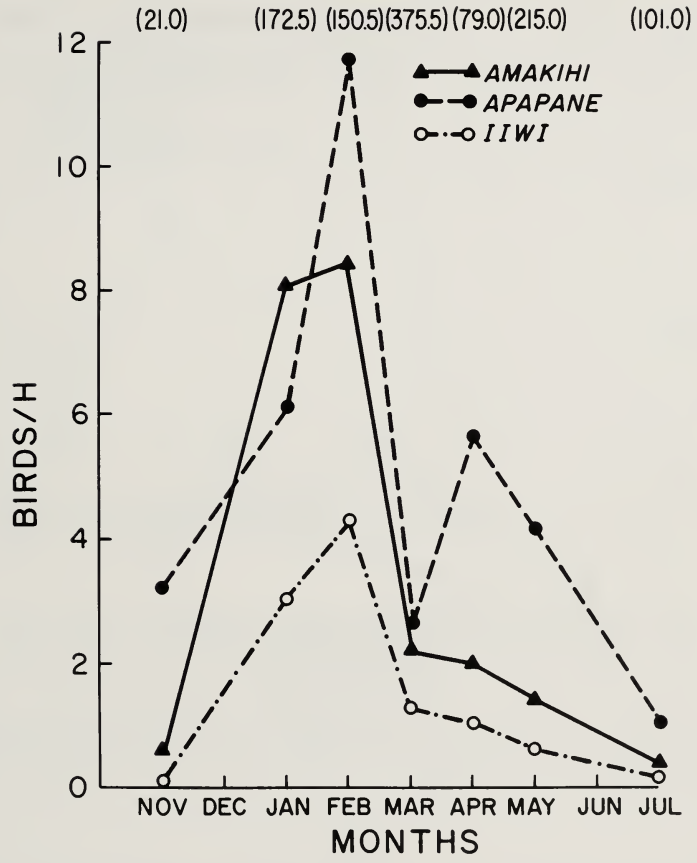


FIG. 2. Average monthly numbers of nectarivorous birds recorded during counts from 1970–1972 in the Kohala Mountain Forest, Hawaii. Numbers at the top in parentheses are sample sizes.

(e.g., Ring-necked Pheasant [*Phasianus colchicus*], Blue Pheasant [*P. versicolor*], Black Francolin [*Francolinus francolinus*] Erckel's Francolin [*F. erckelii*], Grey Francolin [*F. pondicerianus*]).

Unrecorded species.—Noticeably absent from the forest were the Hawaiian Thrush (*Phaeornis obscurus*) (see also van Riper and Scott 1979), and other less common endemics such as the Akepa (*Loxops coccineus*), Akiapolaau and Ou. None of the native species which historically occurred in the forest, but are now believed to be extinct, were observed. Although I did not find evidence of breeding seabirds, Kepler et al. (1979) recently

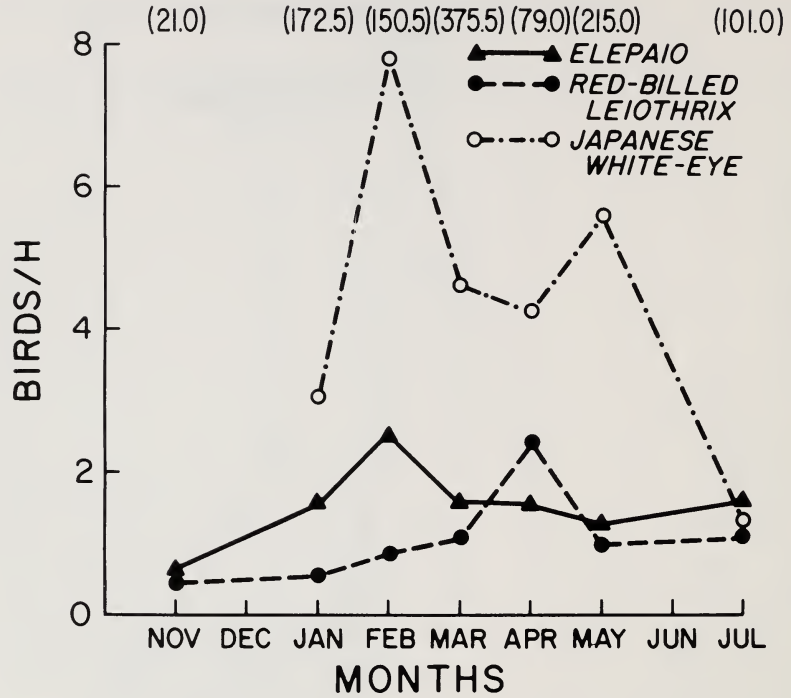


FIG. 3. Average monthly numbers of the common non-nectarivorous passerine species recorded during counts from 1970–1972 in the Kohala Mountain Forest, Hawaii. Numbers at the top in parentheses are sample sizes.

suggested that colonies of Manx Shearwater (*Puffinus puffinus newelli*) may exist in the Kohala Mountain Forest. The Kalij Pheasant (*Lophura leucomelana*) which has recently undergone a great range expansion on the island of Hawaii (Pratt 1975) has apparently not yet reached the Kohala Mountain Forest.

Uniformity of species composition.—In an effort to determine if bird species were uniformly distributed over widespread but similar areas in the Kohala Mountain Forest, comparative counts were undertaken. In all cases no significant difference in species composition existed between outlying areas and the principal study site (Eke: $\chi^2 = 3.54$, df = 8, $P = 0.90$; Kawainui Stream: $\chi^2 = 1.35$, df = 6, $P = 0.97$; Kehena Ditch Trail: $\chi^2 = 1.75$, df = 6, $P = 0.94$). These results suggest that bird species composition is relatively uniform over the extant Kohala Mountain Forest area.

Species abundance.—Overall numbers of most bird species in the Kohala Mountain Forest were higher than comparable studies reported from

TABLE 3
NUMBER OF ACTIVE NESTS FOUND FROM 1969–1972 ON KOHALA MOUNTAIN, HAWAII[a]

Species	Months											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Amakihi	4	10	14	11	8	3	—	—	—	—	—	—
Apapane	—	1	3	4	2	—	—	—	—	—	—	—
Iiwi	—	2	5	4	1	—	—	—	—	—	—	—
Elepaio	—	1	1	2	6	4	3	1	—	—	—	—
Red-billed Leiothrix	—	—	—	1	3	3	1	—	—	—	—	—
Japanese White-eye	—	—	—	1	3	2	1	1	—	—	—	—
Nutmeg Mannikin	—	—	—	1	1	1	—	—	—	1	1	1
Common Mynah	—	—	2	4	3	—	—	—	—	—	—	—
Northern Cardinal	—	4	4	5	2	2	—	—	—	—	—	—
Eurasian Skylark	—	—	1	1	1	—	—	—	—	—	—	—
House Finch	—	—	—	1	4	10	7	—	—	—	—	—
House Sparrow	—	—	2	4	2	—	—	—	—	—	—	—

[a] A nest can occupy more than a 1-month period.

Molokai (Scott et al. 1977) and Oahu (Shallenberger 1978), but lower than other forest areas on the island of Hawaii (Conant 1981b; Scott, pers. comm.). The intermediate numbers of birds recorded during this study may reflect the lowered carrying capacity of this small remnant of now nearly isolated forest. I found that the Apapane was the most abundant bird in the Kohala Mountain Forest, followed closely by the Japanese White-eye and then the Amakihi (Table 1). Not only was the Apapane the most abundant bird over the annual cycle, but it also had the most months when it had the highest relative abundance (Table 2). However, the Amakihi was the most consistently encountered species during count periods in the forest (species frequency = 0.98). The lower species frequency of the Iiwi was primarily a result of its absence during the nonbreeding censuses. However, even when present the Iiwi's relatively low species incidence value indicates that the bird was never commonly encountered.

I analyzed data from all counts conducted within the principal study area and found that numbers of Apapane, Amakihi, and Iiwi changed significantly over the annual cycle (analysis of variance; $P \leq 0.05$; Fig. 2). These three species are all nectarivorous, and their movements in and out of the study area might well be related to changes in local nectar availability as Baldwin (1953) showed was true for another ʻōhiʻa forest on Hawaii. Of the non-nectarivorous species which were encountered frequently enough to determine if population movements occured, none showed significant changes in the number of birds recorded/hour over the

TABLE 4

MEAN PERCENTAGE OF JUVENILE BIRDS RECORDED DURING 1115 H OF CENSUSING FROM 1970–1972 IN THE KOHALA MOUNTAIN FOREST, HAWAII

Species	Month (total hours censused)						
	January (172.5)[a]	February (150.5)	March (375.5)	April (79.0)	May (215.0)	July (101.0)	November (21.0)
Amakihi	2.0	0	0	0	10.0	0	0
(701)[b]	(102)[c]	(67)	(59)	(11)	(31)	(8)	(2)
Apapane	7.0	3.0	0	14.0	59.0	87.0	7.0
(1123)	(69)	(93)	(57)	(28)	(46)	(15)	(15)
Elepaio	3.0	0	0	0	16.0	5.0	75.0
(332)	(36)	(36)	(42)	(9)	(25)	(20)	(4)
Iiwi	53.0	0	0	29.0	50.0	100.0	0
(281)	(19)	(39)	(21)	(7)	(6)	(1)	(0)

[a] Numbers in parenthesis = total hours censused.
[b] Numbers in parenthesis = total birds counted.
[c] Numbers in parenthesis = total visual observations each month.

annual cycle (analysis of variance: $P \geq 0.05$; Fig. 3). These birds tended to be either insectivorous (Elepaio) or omnivorous (Red-billed Leiothrix, Japanese White-eye).

Breeding seasons.—On Kohala Mountain, I found that the native birds tended to nest earlier in the year than did the introduced species (Table 3). The Amakihi showed a more contracted breeding period than has been reported for the population in the dry forest on Mauna Kea (Berger 1972. van Riper 1978b), but had a similar breeding period to the Amakihi from the wet forests of Kauai (Eddinger 1970) and Hawaii (Baldwin 1953). The Apapane and Iiwi had breeding periods similar to those reported from Kauai by Eddinger (1970). I found that the Elepaio had a slightly longer breeding season in the Kohala Mountain Forest than Eddinger (*in* Berger 1972) found for the bird on Kauai, and Conant (1977) found on Oahu.

The breeding seasons of all native species coincided well with immature birds observed during censuses (Table 4). Apapane juveniles were recorded over the longest period, but because it is not yet known the length of time that each of these species retain their juvenal plumage, the same birds may have been observed over an extended time period.

The introduced species on Kohala Mountain all exhibited breeding seasons similar to the limits set for each bird by previous workers. The Japanese White-eye breeding season was within the breeding period of an Oahu population (Guest 1973), but the Red-billed Leiothrix breeding period was later in the year than was given for this bird by Fisher and Baldwin

(1947). The dates of the Common Mynah nests that I found fell within the first third of the breeding season which Eddinger (1967) outlined for an Oahu population. All of the dates for House Finch nests that I located during this study occurred during the same months that other nests have been reported from Hawaii (van Riper 1976) and from Oahu (Hirai 1975). Breeding seasons for the other introduced birds from Kohala Mountain have not yet been determined in Hawaii.

MANAGEMENT RECOMMENDATIONS

Analysis of breeding and census data from the Kohala Mountain Forest shows that, while the present day avifauna is less diverse than historical records indicate, nine native species still exist on the mountain. Four species (Hawaiian Duck, Hawaiian Hawk, Hawaii Creeper, Nukupuu) identified during count periods are classified by the U.S. Fish and Wildlife Service as endangered (USDI 1966). Recent work on a number of endangered species in Hawaii has indicated that genetic fitness may be a problem in rarer species (Walker 1974; van Riper 1980; Temple, pers. comm.). It is therefore imperative that diverse gene pools be preserved in order to insure the genetic integrity of the extant species.

Although the forested area is much reduced in size, the remaining forest does fit a number of criteria Diamond and May (1976) deemed essential for a natural reserve. The forest is nearly circular in shape, which maximizes the area-to-perimeter ratio thus minimizing dispersal distances within the forest. A circular configuration also avoids a peninsular effect in which dispersal rate to outlying parts would be so low as to cause numerous local extinctions thereby diminishing the reserve's effective area. Secondly, the Kohala Mountain Forest has numerous easily accessible stepping stones of forest patches above Honokaa, which lead to the large pristine 'ōhi'a forest on the northeastern flank of Mauna Kea. Over time these forest patches would enable birds to emigrate into the Kohala Mountain Forest area. Finally, because of Hawaii's disharmonic fauna, many forest areas (of which Kohala is one) are well below the carrying capacities of similar-sized islands outlined by Diamond and May (1976) in their review of natural reserves.

The Kohala Mountain Forest area would therefore seem to lend itself well to the reintroduction of certain species which have been extirpated from this region. Translocations of avian species have been carried out quite successfully in New Zealand (Morris 1977, Best 1980), but other than with anatids, little attention has been given to this technique in Hawaii. The Hawaiian Thrush, which was once quite abundant (Perkins 1903) but has now been lost from the Kohala Mountain Forest, would seem to be a prime candidate for reintroduction. The bird still exists in high numbers

on the south and southeastern part of the island (van Riper and Scott 1979), and could be easily captured and transported to the Kohala Mountain Forest.

The Kohala Mountain Forest remains today one of the more inaccessible areas on the main Hawaiian Islands, and because of this can be preserved in its present condition. Barring the introduction of new avian predators, more successful competitors, or an epizootic, the area will remain a refuge for Hawaiian birds. Therefore, steps need to be taken to ensure the preservation of this small, but important native Hawaiian refugium.

SUMMARY

Censuses were conduced from 1970–1972 in the Kohala Mountain Forest, Hawaii. Native passerines were the most commonly encountered birds, with the nectar guild of the Drepanidinae having the greatest numbers of recorded individuals and being the most consistently detected birds. A number of species, known to have occurred historically in the forest, were not found during the study; however, four endangered species (Hawaiian Duck, Hawaiian Hawk, Hawaii Creeper, Nukupuu) were recorded during count periods. The Nukupuu has not been reported previously from the island of Hawaii.

Species composition was constant in the forest throughout the year. However, the nectarivorous species in the principal study area did undergo significant changes in numbers over the annual cycle. The number of non-nectarivorous birds recorded/hour of censusing did not change significantly in the principal study site over the annual cycle. Breeding periods, as determined from active nests and census data, were found to correspond somewhat closely with the presently known breeding season of each species in other areas of Hawaii.

ACKNOWLEDGMENTS

The field phase of this research was made possible by grants from the Frank M. Chapman Fund, Hawaii Audubon Society, and International Council for Bird Preservation. A National Park Service Contract No. CX 8000 7 0009 in conjunction with a National Geographic Society Grant provided partial support during preparation of the manuscript. I thank R. Orenstein, C. John Ralph, J. Michael Scott, and Sandra G. van Riper for their perceptive comments on earlier drafts of this paper.

LITERATURE CITED

Baldwin, P. H. 1953. Annual cycle, environment and evolution in the Hawaiian honeycreepers (Aves: Drepanidinae). Univ. Calif. Publ. Zool. 52:285–398.

Banko, W. E. 1968. Rediscovery of Maui Nukupuu (*Hemignathus lucidus affinis*), and sighting of Maui Parrotbill (*Pseudonestor xanthophrys*), Kipahulu Valley, Maui, Hawaii. Condor 70:265–266.

Berger, A. J. 1972. Hawaiian birdlife. Univ. Press of Hawaii, Honolulu, Hawaii.

———. 1975. The Warbling Silverbill, a new nesting bird in Hawaii. Pacif. Sci. 29:51–54.

Best, H. A. 1980. Recent Kakapo research on Stewart Island. Wildl. Rev. N.Z. Wildl. Serv. 11:33–38.

Conant, S. 1977. The breeding biology of the Oahu 'Elepaio. Wilson Bull. 89:193–210.

———. 1981a. Recent observations of endangered birds in Hawaii's National Parks. Elepaio 41:55–61.

———. 1981b. Organisms along an island mountain transect: birds. Pp. 97–105 *in* Island ecosystems (D. Muller-Dombois, K. W. Bridges, and H. L. Carson, eds.). Hutchinson Ross Publ. Co., Stroudsburg, Pennsylvania.

Diamond, J. M. and R. M. May. 1976. Island biogeography and the design of natural reserves. Pp. 163–186 *in* Theoretical ecology principles and applications (R. M. May, ed.). W. B. Saunders Co., Philadelphia, Pennsylvania.

Donaghho, W. R. 1971. Kohala Mountains scientific expedition. Elepaio 31:101–103.

Eddinger, C. R. 1967. A study of the breeding behavior of the mynah. Elepaio 28:1–15.

———. 1970. A study of the breeding biology of four species of Hawaiian honeycreepers (Drepanidinae). Ph.D. diss., Univ. Hawaii, Honolulu, Hawaii.

Emlen, J. T. 1971. Population densities of birds derived from transect counts. Auk 88: 323–342.

Fisher, H. I. and P. H. Baldwin. 1947. Notes of the Red-billed Leiothrix in Hawaii. Pacif. Sci. 1:45–51.

Guest, S. J. 1973. A reproductive biology and natural history of the Japanese White-eye (*Zosterops japonica japonica*) in urban Oahu. M.S. thesis, Univ. Hawaii, Honolulu, Hawaii.

Hirai, L. T. 1975. The nesting biology of the House Finch in Honolulu, Hawaii. Western Birds 6:33–44.

Kepler, C. B., J. Jeffery and J. M. Scott. 1979. Possible breeding colonies of Manx Shearwater on the island of Hawaii. 'Elepaio 39:115–116.

Morris, R. B. 1977. Black Robin transfers. Wildl. Rev. N. Z. Wildl. Serv. 8:44–48.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. SPSS: statistical package for the social sciences. McGraw-Hill Co., New York, New York.

Perkins, R. C. L. 1901. An introduction to the study of the Drepanidinae, a family of birds peculiar to the Hawaiian Islands. Ibis 1901:562–585.

———. 1903. Vertebrata (Aves). Pp. 368–465 *in* Fauna Hawaiiensis, Vol. 1, Pt. 4 (D. Sharp, ed.). The Univ. Press, Cambridge, England.

Pratt, T. K. 1967. Field notes from Thane Pratt, Kamuela, Hawaii, post marked April 10, 1967. Elepaio 27:112–113.

———. 1975. The Kalij Pheasant on Hawaii. Elepaio 36:66–67.

Rock, J. F. 1913. The indigenous trees of the Hawaiian Islands. Publ. under patronage, Honolulu, Hawaii.

Rothschild, W. 1893–1900. The avifauna of Laysan and the neighbouring islands. R. H. Porter, London, England.

Rottenberry, J. T. and J. A. Wiens. 1976. A method for estimating species dispersion from transect data. Am. Midl. Nat. 95:64–78.

Scott, J. M., D. H. Woodside and T. L. C. Casey. 1977. Observations of birds in the Molokai Forest Reserve, July 1975. 'Elepaio 38:25–27.

Shallenberger, R. J. 1978. Avifaunal survey in the central Koolau Range, Oahu. Ahuimanu Productions, Kailua, Hawaii.

U.S. Department of the Interior. 1966. Rare and endangered fish and wildlife of the United States. Bureau of Sport Fisheries and Wildlife, Research Publication 34.

van Riper, C., III. 1973. Island of Hawaii land bird distribution and abundance. Elepaio 34:1–3.

———. 1974. Unusual uses of Ricebird nests in Hawaii. Elepaio 35:5.

———. 1976. Aspects of House Finch breeding biology in Hawaii. Condor 78:224–229.

———. 1978a. Discovery of the Yellow-fronted Canary on Mauna Kea, Hawaii. 'Elepaio 38:99–100.

———. 1978b. The breeding ecology of the Amakihi (*Loxops virens*) and Palila (*Psittirostra bailleui*) on Mauna Kea, Hawaii. Ph.D. diss., Univ. Hawaii, Honolulu, Hawaii.

———. 1980. Observations on the breeding of the Palila *Psittirostra bailleui* of Hawaii. Ibis 122:462–475.

——— AND J. M. SCOTT. 1979. Observations on distribution, diet, and breeding of the Hawaiian Thrush. Condor 81:65–71.

WALKER, R. L. 1974. 1972 report of Nene restoration program. Elepaio 34:123–127. 135–142.

WILSON, S. B. AND A. H. EVANS. 1890–1899. Aves Hawaiienses: the birds of the Sandwich Islands. R. H. Porter, London, England.

DEPT. ZOOLOGY AND C.P.S.U., UNIV. CALIFORNIA, DAVIS, CALIFORNIA 95616.
ACCEPTED 1 MAR. 1982.

GEORGE MIKSCH SUTTON (1898–1982)

We are saddened to report the passing of Professor George Miksch Sutton at Norman, Oklahoma on 7 December 1982. Professor Sutton most generously endowed the color-plate fund of The Wilson Ornithological Society, was a former president of the Society and a former editor of The Wilson Bulletin.

Wilson Bull., 94(4), 1982, pp. 477–493

OBSERVATIONS OF SOME UNUSUAL RAINFOREST AND MARSH BIRDS IN SOUTHEASTERN PERU

Theodore A. Parker, III

This paper provides information on the behavior, distribution, and taxonomy of 36 species of rainforest and marsh birds found in the tropical lowlands of southeastern Peru. Most species discussed are little-known forest residents, but some are widespread and common in other regions; occurring in Peru only as migrants or vagrants. Observations reported here were made intermittently from June 1977 to October 1981, during which time I spent about 6 months in the Dpto. Madre de Dios.

The most frequently mentioned locality herein is the Tambopata Reserve, a government protected area of 5000 ha on the south bank of the Río Tambopata some 30 km southwest of Puerto Maldonado (12°50′S, 69°16′W). A tourist lodge, the Explorer's Inn, is situated on the reserve at the confluence of the Tambopata and its tributary, the Río La Torre. In recent years this area has attracted many naturalists, particularly ornithologists, who have found an amazing diversity of animals and plants. Within 10 km of the lodge clearing more than 515 bird species have been recorded, of which 90% are residents and 10% are migrants from north or south. An annotated species list for the reserve has been prepared (Donahue et al., unpubl.). To my knowledge this locality supports the richest avifauna in the world.

The Tambopata Reserve lies on generally flat, forested land at an average elevation of about 250 m. Two main types of rainforest exist within the reserve. "Transitional forest" occurs in low-lying, poorly-drained areas not far from the rivers. Much of this habitat is seasonally inundated by overflow from the rivers, or during the wet months of November to April, by heavy rainfall; annual precipitation has been estimated at 1500–2000 mm, and mean annual temperature falls between 18 and 24°C (G. Hartshorn, unpubl.). The canopy here is uneven, averaging about 30 m. Wooded swamps and thickets of bamboo occur in this terrain. Upland or terra firme forest stands on extensive alluvial terraces that rise to 10 m above the seasonally flooded areas. The canopy of upland forest is more continuous than that of transitional forest, but equally high. There is a well-developed understory of short trees and palms in both forest types. One study plot of 1.0 ha in "average forest" on the reserve held 584 trees 10 cm or more in diameter at breast height, representing 153 species, of which only seven were lianas (G. Hartshorn, unpubl.).

Other important habitats on the reserve include shrubby second growth

and thickets of *Gynerium* cane and *Cecropia* trees along banks of rivers, and marsh growth that borders oxbow lakes. Various plants associated with these habitats are mentioned below.

SPECIES ACCOUNTS

Southern Screamer (*Chauna torquata*).—One individual was seen on 15 July 1979, on the muddy south bank of the Río Tambopata 15 km southwest of Puerto Maldonado. This bird was observed for nearly 15 min by L. Barkley, A. Maley, J. Wall, and myself. Local residents were unfamiliar with the species, which is common on the pampas of northern Bolivia only 250 km to the southeast (Gyldenstolpe 1945b). Pearson (1975) reports more northeasterly records in that country. Our sighting and photographs (by Maley) represent a first record for Peru. The Horned Screamer (*Anhima cornuta*) is common along the banks of rivers and around oxbow lakes throughout lowland eastern Peru. It seems to replace *C. torquata* in Amazonia.

Azure Gallinule (*Porphyrula flavirostris*).—In December 1977 and January 1978, this small gallinule was fairly common (up to 10 counted daily) in floating mats of marsh grasses near the waters' edge of Laguna Cococha and Laguna Tres Chimbadas, on and near the reserve, respectively. All individuals seen were in the brownish immature plumage. These birds flushed readily when approached by observers in canoes and dropped back into the vegetation only a few meters farther away. No call notes were given. The small size and dark rump and tail contrasting with a lighter olive-brown back and whitish underparts are characteristic field marks in flight. The larger Purple Gallinule (*P. martinica*) was also present along the lake edges, but they preferred taller, larger-leaved vegetation. On 15 January 1978, A. Mack and I collected an immature *P. flavirostris* at the edge of Laguna Cococha (LSUMZ 87171: skull 70% pneumatized; ovary 8 × 6 mm, ova not enlarged; 68 g; iris amber-yellow; frontal shield and culmen green, rest of bill greenish-yellow; tarsi and feet yellowish-orange). In 1979 the first individual of *P. flavirostris* appeared on Laguna Cococha during the first week of November, and small numbers were observed almost daily through mid-December (T. S. Schulenberg, pers. comm.)

Surprisingly, these are the first records of this species for Peru. Pearson (1975) found this gallinule to be "rare" from November–February at Tumi Chucua, Dpto. Beni, northern Bolivia, and Remsen (unpubl.) considered it a resident near Leticia, Colombia, at the northern border of Peru. Though recorded for the first time in Ecuador only recently (Norton 1965), Tallman et al. (1977) and Ridgely (pers. comm.) have found it to be resident at

Limoncocha, Provincia Napo-Pastaza. *P. flavirostris* may prove to occur, at least seasonally, throughout lowland, eastern Peru.

Rock Parakeet (*Pyrrhura rupicola*).—Forshaw (1978) summarized the scanty available information on this parakeet. The species is fairly common in low-lying and upland forest on the Tambopata Reserve, where observed daily in pairs or, more typically, in groups of 3–8 birds. These are often seen flying just below the treetops. Flying birds characteristically remain in a tight group; they flap rapidly several times and then glide a short distance before flapping again, giving raspy, high-pitched flight calls *kriik-kriik-kriik*. Occasionally, members of groups perched in dense foliage high in trees utter shrill *kreee* notes reminiscent of some vocalizations of the White-bellied Parrot (*Pionites leucogaster*), another common bird of the reserve. *Pyrrhura rupicola* is known from only a few scattered localities in southeastern Peru, southwestern Brazil, and northern Bolivia (Forshaw 1978). Meyer de Schauensee (1966, 1970) gives the "subtropical zone" as the elevational range of this parakeet. In fact, it inhabits lowland and hill forest in the "tropical zone" east of the Andes. To my knowledge the species is not sympatric with any other *Pyrrhura*; it apparently replaces forms of the Painted Parakeet (*Pyrrhura picta*) between Dpto. Junín, Peru, and Dpto. La Paz, Bolivia.

Ash-colored Cuckoo (*Coccyzus cinereus*).—One of these distinctive cuckoos was observed on 13 July 1977, in transitional forest on the reserve by S. A. Parker, P. Alden, and myself. The bird was hopping along branches and vines in the lower canopy of a tall forest tree, and was apparently associating with a mixed-species flock that included Chestnut-winged Hookbills (*Ancistrops strigilatus*), Rufous-tailed Xenops (*Xenops milleri*), Spot-winged Antshrikes (*Pygiptila stellaris*), and numerous tanagers, honeycreepers, and greenlets. The cuckoo was carefully watched for at least 10 min; the *Coccyzus* behavior, overall grayish coloration, reddish eye, and rather short, square, white-tipped tail were marks noted at the time. *C. cinereus* was until now known to range north in western South America as far as Dpto. Beni (Gyldenstolpe 1945b). It breeds mainly in the Chaco of Paraguay and northern Argentina (Short 1975) and is probably only an austral winter visitor north of that region.

Least Pygmy-Owl (*Glaucidium minutissimum*).—On the Tambopata Reserve this owl is regularly heard, especially in clearing edge and river edge woodland, where syntopic with Ferruginous Pygmy-Owl (*G. brasilianum*). Unlike the latter, however, Least Pygmy-Owls are also found in the interior of transitional and upland forest. Individuals sing most often at dawn and dusk, but also sporadically through the day and night. The song consists of a descending series of about six soft whistles. *G. minutissimum*

has been previously reported from only two Peruvian localities (O'Neill 1969, O'Neill and Pearson 1974), but recently it has also been found in Manu National Park, Dpto. Madre de Dios (Terborgh et al., unpubl.). The species is probably widespread, but often overlooked, in Amazonia.

Pale-breasted Spinetail (*Synallaxis albescens*).—Between mid-July and mid-August 1979, and again from 1–3 November 1979, several of these spinetails were present in tall grass under willows (*Salix* sp.) and other trees and shrubs (especially *Tessaria* sp.) on a sand bank of the Río La Torre near its junction with the Río Tambopata. The birds were observed by P. Donahue, T. Schulenberg, myself, and many others. These individuals of *S. albescens* were elusive and not at all vocal; they remained in grass until flushed into nearby trees and shrubs. A specimen referable to the southern race *australis* was netted on 20 August 1979 (LSUMZ 92153: skull 30% pneumatized; ovary not enlarged; 9 g; iris reddish-brown; maxilla slate, mandible silvery-gray; tarsi and feet olive-yellow). These records of *S. albescens* are the first for Peru. An earlier report (Meyer de Schauensee 1966) is erroneous (*fide* Manuel Plenge). The species was known to occur as close to Peru as the Dpto. Beni, Bolivia (Gyldenstolpe 1945b) and near Leticia, on the Colombian bank of the Amazon (Remsen unpubl.; specimen, Museum of Vertebrate Zoology). It is not known whether the birds noted on the reserve were residents or migrants from the south.

Peruvian Recurvebill (*Simoxenops ucayalae*).—This distinctive ovenbird is uncommon or rare on the reserve. It frequents dense undergrowth 0.5–4 m above ground in low-lying forest and is seen singly, in pairs or groups of 3–4 individuals. The species seems to favor bamboo thickets, but it is not restricted to them. They hop along branches and trunks of fallen trees and understory palms, and M. Robbins (pers. comm.) saw them hammering dead bamboo stalks, presumably to dislodge prey items. The call is a loud *chek* or *chack*, and what is presumably the territorial song consists of a rising and accelerating series of these notes given in rapid succession. This latter vocalization is similar in pattern and quality to the territorial songs of foliage-gleaners of the genus *Syndactyla*, the Buff-browed Foliage-gleaner (*S. rufosuperciliata*), and the Lineated Foliage-gleaner (*S. subalaris*). Six specimens (LSUMZ 84720, 86398, 86399, 87887, 98023, 98302) of *S. ucayalae* were collected on the reserve, on 20 and 23 July 1977, 5 January 1978, and 8 June and 19 November 1980. Two adult males and one adult female (crania fully pneumatized, gonads not in breeding condition) collected in July weighed 50, 50, and 53 g, respectively. A female collected by J. P. O'Neill at Balta (300 m), on the Río Curanja, Dpto. Loreto, 3 April 1971 (ovary not enlarged) weighed 55 g. Perishable colors of specimens with fully pneumatized crania were as follows: iris dull gray-brown (1 ♂) or dark brown (1 ♀, 1 sex?); maxilla

gray with blackish base (1 ♂), dark olive-gray (1 ♀), or slate-black (1 sex?); mandible silvery-blue (1 ♂), silvery (1 ♀), or bluish-gray (1 sex?); tarsi and feet olive-green (1 ♂, 1 ♀) or grayish-green (1 sex?). A female taken by M. Robbins on 19 November had the cranium 80% peneumatized; it differed from the specimens listed above in having a horn-colored maxilla. A juvenile (sex?) taken on 5 January weighed 51 g. It is much paler than the adults, being buffy below with the breast and belly feathers tipped dusky-brown; the throat is distinctly whitish with dusky-brown tips to some feathers; the superciliary line is buff as opposed to rufous of the adult; the crown and back are only slightly paler than the adult. This plumage has been described only recently (Vaurie 1980). *S. ucayalae* was known from fewer than 10 specimens from only two other localities in Peru (O'Neill 1974), but it has recently also been found in Manu National Park (Terborgh et al., unpubl.).

Brown-rumped Foliage-gleaner (*Automolus melanopezus*).—An uncommon or rare bird on the reserve, this inconspicuous furnariid inhabits lowlying forest where it seems to be closely associated with bamboo. Individuals and pairs were found in at least four large thickets of *Guadua* bamboo, where they frequented dense cover from 3–8 m above ground. The species occasionally associated with mixed-species flocks, especially those comprised of the Ornate Antwren (*Myrmotherula ornata*), Striated Antbird (*Drymophila devillei*), and Warbling Antbird (*Hypocnemis cantator*). The song of *A. melanopezus* is comprised of two emphatic introductory notes followed by a rapid succession of harsh notes (*whit-whit-wut-trrrrrrrr*) about 3 sec long. One specimen was netted in dense undergrowth near a forest stream (LSUMZ 87895: 5 Jan. 1978; skull fully pneumatized; testes 11 × 8 mm; 30.5 g; iris red; bill dusky-gray; tarsi and feet olive-green); and another was netted in bamboo (LSUMZ 98303: 13 Nov. 1980; skull pneumatized; testes 14 × 6 mm; heavy body molt; no weight; iris reddish-brown; bill horn-colored; tarsi and feet yellowish-gray; taken by M. Robbins). Though this species is probably widespread in Amazonian Peru, there is only one published record for the country (O'Neill 1969). Terborgh et al. (unpubl.) also list *A. melanopezus* from Manu National Park.

Rufous-tailed Xenops (*Xenops milleri*).—This relatively large *Xenops* can be observed daily in small numbers in both transitional and terra firme forest on the reserve. It is nearly always seen with mixed-species flocks of tanagers, greenlets, and antwrens that move through the canopy and subcanopy. In contrast to the syntopic Plain Xenops (*X. minutus*), which in this area is mainly an undergrowth and lower middlestory species, *X. milleri* is usually observed 15–25 m above ground. The species forages by hopping along bare, slender branches and vines (usually not exceeding 2 cm in diameter) and constantly turning from side-to-side; prey items are

often gleaned from the sides and undersurfaces of branches. Though no specimens were obtained, *X. milleri* can be instantly recognized by its buffy, heavily streaked underparts, and its lack of a silvery malar steak. The Rufous-tailed Xenops was known from only a few localities in Amazonia, and only one from Peru (Peters 1951).

Sclater's Antwren (*Myrmotherula sclateri*).—Although inconspicuous, this antwren is common in the canopy of transitional forest, and uncommon in canopy of terra firme. Pairs live amidst dense foliage and vine tangles at least 12 m above ground. These birds glean stems and leaves, and occasionally pick at spider webs and bark of branches and vines. The song is a series of plaintive, whistled *peer* notes repeated 3–6 times with only short intervals between them; these series are usually given about 5 sec apart. This vocalization can be mistaken for the song of the Fasciated Antshrike (*Cymbilaimus lineatus*), which occurs in the same habitat. In response to playback, both male and female of a pair of *M. sclateri* will descend to within about 8 m of the ground. The disturbance call is a soft, but oft-repeated *wit*. These antwrens occasionally follow mixed-species flocks of other antwrens, honeycreepers, and tanagers. *M. sclateri* overlaps ecologically with the very similarly-colored Pygmy Antwren (*M. brachyura*). The latter, however, seems to prefer disturbed forest (i.e., edges of treefall clearings) and may not normally forage as high as *M. sclateri*. Sclater's Antwren was previously known from one locality in Peru (O'Neill 1969), and only a few other localities in Amazonia (Meyer de Schauensee 1966).

Ihering's Antwren (*Myrmotherula iheringi*).—This antwren is seemingly the rarest *Myrmotherula* on the reserve. The species is closely associated with bamboo, though it was also seen in adjacent forest undergrowth. *M. iheringi* is invariably noted in pairs moving through the crowns of bamboo thickets, often in the company of the Ornate Antwren (*M. ornata*) and the White-eyed Antwren (*M. leucophthalma*). The song of *M. iheringi* is a long series of 18–25 *peeu* notes uttered at short intervals on one pitch. A specimen secured in bamboo (LSUMZ 98335: 1 November 1980; skull pneumatized; testes 3 × 2 mm; 7.5 g; iris dark brown; bill black; tarsi and feet gray) by M. Robbins verifies the occurrence of this species in Peru. Munn and Terborgh (1979) list *M. iheringi* as an occasional member of mixed-species flocks in Manu National Park. Ihering's Antwren was previously known from only a few localities in western Brazil (Meyer de Schauensee 1966).

Striated Antbird (*Drymophila devillei*).—Like its Andean relative the Long-tailed Antbird (*D. caudata*), this beautiful bird appears to be dependent on bamboo for cover. The species is found in pairs or family groups

in the dense crowns of thickets 2–7 m above ground. Individuals hop deliberately along bamboo branches, picking insects, especially small caterpillars, off nearby leaves, bark, and *Tillandsia*-like epiphytes. They occasionally lunge out and sally-glean a prey item from a surface up to 30 cm away. While foraging they often jerk their tails from side-to-side and utter soft *chip* or *chep* notes. The territorial song of the male is an explosive, very raspy series, *bzeent-bzeet-bzeet-zeet-tititiri*. A similar version of this vocalization is given by the female, usually in response to the male's song. The songs and calls of this species are much like those of *D. caudata* of the Andes, the Ochre-rumped Antbird (*D. ochropyga*), and Rufous-tailed Antbird (*D. genei*) of southeastern Brazil.

The spotty distribution of *D. devillei* in Amazonia (Peters 1951) surely reflects the patchiness of the bird's habitat. A variety of other birds found on the reserve seem to be closely associated with bamboo; these include such diverse forms as the Rufous-headed Woodpecker (*Celeus spectabilis*), *S. ucayalae*, *M. ornata*, Large-headed Flatbill (*Ramphotrigon megacephala*), Flammulated Pygmy-Tyrant (*Hemitriccus flammulatus*), and Slate-colored Seedeater (*Sporophila schistacea*).

It is interesting to note that the close relatives of *D. devillei*, *Hemitriccus flammulatus*, and *S. schistacea* (i.e., *D. ochropyga*, Drab-breasted Pygmy-Tyrant [*Hemitriccus diops*], and Temminck's Seedeater [*Sporophila falcirostris*]), are found in bamboo in montane or subtropical areas from southeastern Brazil to northeastern Argentina. This suggests that certain bamboos were an important floristic element in a relatively cool, humid forest that may have once extended from the Andes to the Atlantic south of Amazonia proper. Other taxa that are associated with bamboo (pers. obs.) and that show similar disjunct distributions across the South American continent include the Maroon-chested (*Claravis mondetoura*) and Purple-winged (*C. godefrida*) ground-doves, Buff-browed Foliage-gleaner (*Syndactyla rufosuperciliata*), Giant Antshrike (*Batara cinerea*), Slaty (*Haplospiza rustica*) and Uniform (*H. unicolor*) finches, and Blue (*Amaurospiza concolor*) and Blackish-blue (*A. moesta*) seedeaters.

Chestnut-shouldered Antwren (*Terenura humeralis*).—This small, warbler-like antbird is an inconspicuous member of mixed-species flocks in the canopy of both transitional and terra firme forest on the reserve. Usually encountered in pairs, these birds are most often seen near the ends of branches where they glean leaves. In the field they may easily be confused with greenlets (*Hylophilus*), especially the syntopic Dusky-capped Greenlet (*H. hypoxanthus*). *T. humeralis* can be located by listening for its territorial song, a high-pitched series of chipping notes that speeds to a trill towards the end. In response to playbacks of this vocalization, males

will descend to within 8 m of the ground and counter-sing; when excited, their chestnut lower back feathers become quite conspicuous. A soft disturbance *wit* is also uttered. *T. humeralis* is very similar in voice and behavior to at least three of the four other *Terenura*, the Rufous-rumped Antwren (*T. callinota*), Yellow-rumped Antwren (*T. sharpei*), and Ash-winged Antwren (*T. spodioptila*); the fourth, the Steaked-capped Antwren (*T. maculata*), has quite a different song, but it too is a canopy-dwelling, flock-following species. Though I was unable to collect a specimen of *T. humeralis*, it is the only member of its genus known from lowland Peru (from only one record, Peters 1951). The species has also been taken in adjacent southwestern Brazil (Gyldenstolpe 1945a).

Band-tailed Antbird (*Hypocnemoides maculicauda*).—This antbird and the Silvered Antbird (*Sclateria naevia*) are restricted to the edges of wooded swamps and oxbow lakes, and seasonally flooded forest, where *Hypocnemoides* frequents overhanging or emergent branches of fallen trees within a few centimeters of water. *Sclateria*, in contrast, hops on leaf litter and logs at the water's edge. Numbers of both species increase dramatically along the edges of oxbow lakes during the dry season (July–October) when many woodland streams and swamps dry up. *H. maculicauda* gleans insects off branches, and occasionally sally-gleans prey from the ground or water. The song of the species is very like that of its northern counterpart the Black-chinned Antbird (*H. melanopogon*), but is longer and has an introductory component not given by individuals of *melanopogon* in Venezuela (pers. obs. from recordings of the latter by P. Schwartz in the LNS). The song of *H. maculicauda* is a rising, accelerating series that ends abruptly with several raspy notes, *pee-pee-pee-pee-pipipipipi bzzt-bzzt-bzzt-bzzz*. The Band-tailed Antbird is widespread in Amazonia south of the Marañón and Amazon rivers (Meyer de Schauensee 1966), but it is relatively scarce in collections from Peru.

White-lined Antbird (*Percnostola lophotes*).—Individuals of this species have evidently been described as two different species. Hellmayr and Seilern (1914) gave what was almost certainly an immature male the name *P. lophotes*. Then Berlioz (1966) described a single adult male as *P. macrolopha*. S. A. Parker and I netted a male and female together on the Tambopata Reserve, and we compared our specimens (LSUMZ 84891, 84892) with the respective descriptions cited above. Hellmayr and Seilern's (1914) description of the male agrees closely with our female-plumaged specimen, with the exception of the blackish primary coverts of their bird, a characteristic of male *lophotes*. Our male *lophotes* is nearly identical to that described by Berlioz (1966).

P. lophotes is a fairly common inhabitant of low, damp thickets of *Guadua* bamboo and *Gynerium* cane in low-lying forest and along the river edges on the reserve. Nearly always observed in pairs, these antbirds hop

slowly through the undergrowth and glean foliage and bark of slender branches and trunks from 0.5–2 m above ground. They constantly flick the tail down and raise it slowly, lifting the closed wings in the process. The long crest is held conspicuously erect much of the time, especially when birds have been disturbed. The primary vocalization is a loud, far-carrying series comprised of an introductory *kep* followed by a descending (bouncing) succession of *kup* notes (*kep kup-kup-kup-kup-p-p-ppp*). This song is uttered by territorial males from dawn until about 08:30 on clear days; the female gives a similar song in response to that of the male. The call is a loud, slightly nasal *aaah*. Calling birds perch upright, with neck outstretched and bill pointed upwards, slowly raising and lowering their crests. Once, after I played back songs of a pair, the birds sat side-by-side, about 3 cm apart, and pecked at exposed areas of skin on the neck and head of their mate.

In both vocalizations and behavior *P. lophotes* is reminiscent of certain antshrikes (*Thamnophilus* spp., *Sakesphorus* spp.), and it is quite unlike two other supposed congeners, the Spot-winged Antbird (*P. leucostigma*) and the Black-headed Antbird (*P. rufifrons*). *P. leucostigma* utters a peculiar trilled song, and *P. rufifrons* whistles a musical series of notes reminiscent of the song of Goeldi's Antbird (*Myrmeciza goeldii*). To my knowledge, neither utters the *Thamnophilus*-like *aaah* notes of *P. lophotes*. I suspect that the three *Percnostola* listed above will eventually be shown not to be congeneric. Five specimens of *P. lophotes* (LSUMZ 84891–84893, 92421, 99371) were mist-netted on the reserve on 17, 19, and 20 July 1977, 1 November 1978, and 8 December 1980. An adult male and an adult female (crania fully pneumatized; gonads not in breeding condition) collected in July weighed 33.5 and 30 g respectively. Soft-part colors of these individuals were as follows: iris dark brown (male) and reddish-brown (female); maxilla black (male) and dusky black with silvery tomium (female); mandible black (male) and silvery-gray (female); tarsi and feet medium gray (male, female). The iris color in two other adult males (with fully pneumatized crania) differed in being gray, and gray with reddish flecks around the pupil. *P. lophotes* was previously known from only four examples from three localities in southern Peru (Meyer de Schauensee 1966); recently it has also been found in Manu National Park (Terborgh et al., unpubl.).

Goeldi's Antbird (*Myrmeciza goeldii*).—The loud, whistled song of this large antbird is a characteristic sound of low-lying forest on the reserve. This uncommon species frequents open to moderately dense undergrowth, including bamboo, from the ground to about 2 m above it. A nest found on 30 September 1980, was on the ground amidst dense undergrowth of bamboo and cane; the cup of dried leaves and twigs measured about 18 cm in diameter and contained a single, white egg, with irregular blotches

of reddish-brown coloration over its entire surface. Both male and female took turns incubating this egg, which disappeared from the nest 5 days after discovery (M. Robbins, pers. comm.). The song is a ringing, whistled *piti-peeur-peeur-peeur-peeur* delivered from a perch 1–3 m above ground. A loud *kep-kep* is also part of the repertoire; this vocalization, I believe, is a disturbance or alarm call. The songs and calls of *M. goeldii* are very similar to those of the White-shouldered Antbird (*M. melanoceps*). As in the case of the Bluish-slate Antshrike (*Thamnomanes schistogynus*) and the Cinereous Antshrike (*T. caesius*), where females differ strikingly in color pattern, these antbirds replace each other ecologically and geographically. Six specimens of *M. goeldii* (LSUMZ 84908–84910, 86407, 92422, 98346) were mist-netted on the reserve on 19, 21, and 23 July 1977, and 15 November 1980. Two adult males and two adult females (with fully pneumatized crania; gonads not enlarged) collected in July weighed 48.5, 41, 43, and 43 g, respectively. An unsexed bird (female by plumage) from the same month weighted 40 g. Typical perishable colors in both sexes were as follows: iris crimson red; bill black; tarsi and feet blue-gray; exposed facial skin blue-gray. An adult female collected on 15 November by M. Robbins was in reproductive condition, with one ovum 10 × 9 mm.

M. goeldii was previously known from only three localities, two in Brazil and one in eastern Peru (O'Neill 1969). It has also recently been found in Manu National Park (Terborgh et al., unpubl.)

Striated Antthrush (*Chamaeza nobilis*).—As with the Short-tailed Antthrush (*C. campanisona*), this species is best detected by its voice. *C. nobilis* is apparently rare on and near the reserve as there are only six records for the area. I observed two different individuals in July 1979; both were walking on the ground in tall forest with sparse undergrowth. One of these birds was singing, and in response to playbacks of its own voice, the bird approached and walked in semicircles about 10 m in front of me. The song is similar to that of *C. campanisona* in having an accelerating introductory series of hollow whistles followed by a terminal succession of rather harsh *wah* notes. The entire sequence is about 8 sec long, being generally higher-pitched and faster than that of *C. campanisona*.

C. nobilis is widespread, but perhaps local in Amazonia (Meyer de Schauensee 1966). The above records are the southernmost for the species, which has recently been observed in Manu National Park (Terborgh et al., unpubl.) as well.

Ash-breasted Gnateater (*Conopophaga peruviana*).—I have little information on this poorly known species, though it is present in small numbers in transitional forest on the reserve. On one occasion in January 1978, I taped the call note, a loud *chink*, of an immature male, and in response to playbacks the bird hopped about me in the open undergrowth (about 1 m above ground) and held its striking white postocular tufts straight out

from its head. All my observations have been of individuals perching 0.5–1 m above ground, usually sideways on the trunks of slender saplings or on branches of fallen trees. This report is the southernmost for *C. peruviana*.

Yellow-browed Tyrant (*Satrapa icterophrys*).—On 15 June 1977, I saw one of these flycatchers in shrubby second-growth on the outskirts of Puerto Maldonado. Another very worn individual was noted on 21 June 1977, in bushes at the marshy edge of Laguna Cocococha on the reserve. From mid-July to mid-August 1979 at least six *Satrapa* were present in a small area of *Salix* and *Tessaria* trees along the Río La Torre. These birds seemed to be associating with other flycatchers including Rufous Casiornis (*Casiornis rufa*), Short-crested Flycatcher (*Myiarchus ferox*), and Plain Tyrannulet (*Inezia inornata*), all of which, with the probable exception of *M. ferox*, were probably migrants from the south. One *S. icterophrys* was seen there as late as 14 November 1979 (T. S. Schulenberg, pers. comm.). Several *Satrapa* were also noted in this same area from June until mid-September 1980, after which time they disappeared (M. Robbins, pers. comm.). The species perched in foliage of trees and shrubs from 1–7 m above ground, and made outward sally-gleans to foliage and twigs. Prey included numerous caterpillars at least 1 cm in length. One specimen of *S. icterophrys* was netted in the willows (LSUMZ 92728: 22 July 1979; skull fully pneumatized; testes 3 × 2 mm; 18 g; stomach full of insect remains; iris medium brown; bill black; tarsi and feet black). Peru was not included in the range as given by Meyer de Schauensee (1966, 1970), but Traylor (1979) reported the occurrence of this species in the country without giving exact localities. Eventually, *S. icterophrys* may prove to be a widespread, uncommon visitant to lowland eastern Peru.

Rusty-margined Flycatcher (*Myiozetetes cayanensis*).—This flycatcher is apparently resident in small numbers in marsh vegetation at the edges of Laguna Cocococha, Laguna Tres Chimbadas, and Laguna Cochachica on the reserve. It was first found by R. S. Ridgely on 30 June 1978, and has subsequently been seen constantly by many observers. Tape recordings made on the reserve of the distinctive call of the species, a clear, down-slurred whistle, are on deposit in the LNS. This is the first report of the Rusty-margined Flycatcher for Peru, though it has been taken in adjacent northern Bolivia (Meyer de Schauensee 1966).

Rufous Casiornis (*Casiornis rufa*).—During July–August 1979 one or two of these tyrannids were regularly observed in riparian growth (see account of *S. icterophrys*) along the Río La Torre. The birds perched 1–7 m above ground and made 0.5–2 m forward and upward sallies to glean foliage. No vocalizations were heard. One specimen was netted (LSUMZ 92749: 22 July 1979; skull fully pneumatized; testes 2 × 1 mm; 19 g; iris medium brown; bill gray-brown, basal one-half flesh-pink; tarsi and feet grayish-

black). This is the second reported occurrence in Peru of this species (see Parker and O'Neill 1980).

White-cheeked Tody-Flycatcher (*Poecilotriccus albifacies*).—On 19 August 1979, I briefly observed a female of this species as it perched and foraged 2 m above ground in a bamboo thicket along the main trail on the reserve. Thereafter, a pair was regularly seen in the same area through late October 1981, at which time I knew of the presence of two additional pairs on the reserve, and two others in adjacent areas. *P. albifacies* seems to be entirely restricted to *Guadua* bamboo. Most observations were of pairs that remain within the crowns of thickets from 3–9 m above ground. Typical foraging movements include 3–6 cm upward and forward sally-gleans of bamboo foliage and branches. Though normally they perch upright, occasionally individuals will hop along a branch and perch-glean nearby surfaces. The frequently heard call of *P. albifacies* is an emphatic *tick-picpicpicpicpic*, which is given by both sexes. Vocally, and in terms of foraging behavior, this species is quite reminiscent of another bamboo-inhabiting flycatcher, the Flammulated Pygmy-Tyrant (*Hemitriccus flammulatus*). Only one specimen of the White-cheeked Tody-Flycatcher has been reported to date (Blake 1959), though a small series was recently collected by J. W. Fitzpatrick (unpubl.) and a single male was obtained by M. Robbins (unpubl.), all from extreme southeast Peru.

White-lored Tyrannulet (*Ornithion inerme*).—This tiny flycatcher is fairly common on the reserve, but very difficult to observe. Its song is a persistently repeated, high pitched *whee-whee-whee-whee-whee* uttered from a treetop perch, often over wooded swamps or at the edges of clearings and oxbow lakes. In response to playbacks, individuals sometimes descend to within 10 m of the ground and give a buzzy, trilled call. A specimen was netted in transitional forest undergrowth by T. Schulenberg on 9 November 1979 (LSUMZ 92889; skull 40% pneumatized; testes 5 × 3 mm; 7 g; iris brown; bill and tarsi black). The species was not known to range south of Dpto. Pasco and Dpto. Loreto (Traylor 1979). *O. inerme* is probably widespread and not uncommon in Amazonia, and it no doubt occurs in northern Bolivia.

Subtropical Doradito (*Pseudocolopteryx acutipennis*).—In mid-July 1979, several of these flycatchers were found in meter high grass under *Salix* and *Tessaria* trees near the bank of the Río La Torre. When flushed, individuals flew rapidly low over the grass and dropped back 10 m or more away. One specimen (LSUMZ 92825: 22 July 1979; skull 50% pneumatized; testes not enlarged; 6 g; stomach with insects including beetle parts; iris brown; maxilla black, mandible flesh-colored; tarsi and feet gray) was flushed into a net. These records are the first for Peru away from the Andes, and the birds were probably migrants (see Traylor 1979).

Plain Tyrannulet (*Inezia inornata*).—This species was common in *Salix* and *Tessaria* trees along the Río La Torre in July–August 1979, from June through late September 1980, and from late May to late October 1981. In this locality, Plain Tyrannulets were encountered in groups of up to six birds in association with other flycatchers (see under *S. icterophrys*). *Inezia* resembled a warbler (*Vermivora* sp.) or kinglet (*Regulus* sp.), gleaning and hover-gleaning foliage at all heights in trees. Two specimens were mist-netted on 22 July 1979 (LSUMZ 92838: skull fully pneumatized; ovary 2 × 2 mm; 4.5 g; iris brown; bill dark horn; tarsi and feet slate-colored; LSUMZ 92839: skull pneumatized; ovary 3 × 2 mm; 5.5 g; iris brown; bill dark horn, base of mandible flesh-colored; tarsi and feet gray). Traylor (1979) gave the first record for Peru, also from Dpto. Madre de Dios. The species is almost surely an austral migrant in southeastern Peru.

Buff-breasted Wren (*Thryothorus leucotis*).—Two specimens (LSUMZ 88581, 92976) of this wren were netted, one in low secondary growth at the edge of the lodge clearing by B. Sorrie and the other in dense vegetation at the edge of a small lake by E. Mackrill. A few others have been seen and tape-recorded in shrubbery along the edge of Laguna Tres Chimbadas. The above specimens have been compared to examples of *leucotis* from farther north (Pucallpa, Dpto. Loreto) and the Fawn-breasted Wren (*T. guarayanus*) from farther south (Riberalta, Dpto. Beni, Bolivia). The Tambopata specimens agree closely with examples of *T. l. peruanus* from central Peru, and thus represent a southerly range extension for that form. *Thryothorus guarayanus* specimens from Riberalta differ from *T. l. peruanus* in having shorter bills, grayer crowns and backs, and generally slightly paler underparts, but are otherwise quite similar to that form. Pearson (1975), and Remsen and Ridgely (pers. comms.) found *guarayanus* in edge habitats like those of *leucotis* in Peru.

Veery (*Catharus fuscescens*).—An individual of this thrush was seen on 5 November 1980 at the edge of a bamboo thicket (M. Robbins, pers. comm.). The bird was well seen at 10 m; the observer noted its rusty upperparts, lack of an eye-ring, and a buffy wash on an indistinctly marked breast. This is the first report of *C. fuscescens* in Peru. The species is known to range south to Mato Grosso in Brazil (Meyer de Schauensee 1966) and Bolivia (Remsen and Ridgely 1980).

Creamy-bellied Thrush (*Turdus amaurochalinus*).—This thrush occurs in small numbers in Peru from June to October; it is apparently a migrant from the south. On the reserve the species is most often seen near or on the ground at clearing edges, and in the *Salix-Tessaria* growth along the Río La Torre. I have not heard the species sing in Peru. The LSUMZ has 15 specimens of *T. amaurochalinus* taken from Dpto. Loreto (Balta, Río Curanja), and several localities in Dpto. Madre de Dios; these were

collected from 15 June (Balta)–3 October (105 km west of Puerto Maldonado). The species was previously recorded in Peru only from Dpto. Puno (Meyer de Schauensee 1966).

Lawrence's Thrush (*Turdus lawrencii*).—Despite its spotty distribution in Amazonia (Meyer de Schauensee 1966), this species is fairly common on the reserve. Anyone visiting the area should soon hear the song of this bird, which consists of a very long continuous series of near-perfect imitations of portions of songs and call notes of other bird species. As many as 35 bird species are imitated by some individuals of *T. lawrencii*. These range from the ground-dwelling Little Tinamou (*Crypturellus soui*) and Black-faced Antthrush (*Formicarius analis*) to Warbling Antbird, Chestnut-tailed Antbird (*Myrmeciza hemimelaena*) and *M. goeldii* of the undergrowth, and Black Hawk-Eagle (*Spizaetus tyrannus*), White-bellied Parrot and Slate-colored Grosbeak (*Pitylus grossus*) of the middlestory and canopy. Territorial individuals of *T. lawrencii* sing these songs from a few frequently used perches high in the canopy and subcanopy of seasonally flooded forest, and over streams in terra firme. Most territories include a portion of a wooded swamp or forest stream; the thrushes forage in leaf litter at the edges of these habitats, and they also feed on small fruits plucked in flight from trees. I was unable to collect any of these birds, but their uniform brown coloration, white belly, and distinctive yellow bill and eye-ring make field identification easy. Lawrence's Thrush was known in Peru only from the northeast (Meyer de Schauensee 1966), but it has been taken on the Río Purús in southwestern Brazil (Gyldenstolpe 1951).

Pale-eyed Blackbird (*Agelaius xanthophthalmus*).—This blackbird is found in small numbers in floating marsh grasses and scattered bushes along the margins of Laguna Tres Chimbadas northeast of the reserve. The species is most easily seen in early morning when singing individuals perch atop bushes protruding above the grass. The song, *tew-tew-tew-tew*, is somewhat like that of the Black-capped Mockingthrush (*Donacobius atricapillus*), a common marsh inhabitant in the area, but it has a more piercing quality and is much less variable. The call note is a dry *chek*, like that of the Red-winged Blackbird (*A. phoeniceus*), but softer. Presumed immature birds, brown in coloration with yellowish, brown-streaked breasts, were also seen in the area. Only the uniform black adult plumage has been described (Short 1969). This uncommon, local icterid is now known from five localities in western Amazonia: Tingo Maria, Dpto. Huánuco, Peru, the type locality (Short 1969); Limoncocha, Prov. Napo-Pastaza, Ecuador (Tallman et al. 1977); Rioja, Dpto. San Martín, northern Peru (unpubl., and those of G. R. Graves); Manu National Park, Dpto. Madre de Dios (Terborgh et al., unpubl.); and from the reserve.

Flame-crested Tanager (*Tachyphonus cristatus*).—This wide-ranging Amazonian tanager is a common and conspicuous member of mixed-species flocks in the canopy of low-lying forest on the reserve. A specimen (LSUMZ 85490: 29 June 1977; skull fully pneumatized; testes enlarged; 23 g) from the nearby Río Heath is of the race *madeirae*. This is the first report of this form in Peru. *T. cristatus* apparently replaces the Yellow-crested Tanager (*T. rufiventer*) in southern Peru; the latter is common in Manu National Park only 150 km to the northwest.

Red-billed Pied-Tanager (*Lamprospiza melanoleuca*).—I have four records of this distinctive tanager on the reserve. All were of one to three birds associating with mixed-species flocks or aggregations of small birds in the canopies of fruiting trees in terra firme forest. The species was previously known from only two localities in Peru (Pearson 1975), but has also been found in Manu National Park (Terborgh et al., unpubl.). It has a wide range in northern South America, but apparently occurs in low densities, and may be local.

Yellow-shouldered Grosbeak (*Caryothraustes humeralis*).—Only recently reported for the first time in Peru (Parker and O'Neill 1980) and Bolivia (Remsen and Ridgely 1980), this bird was seen three times on the reserve in transitional forest. All records were of single birds in the company of tanagers, honeycreepers, and greenlets high in the canopy. Though my observations were brief, the grosbeaks appeared to be gleaning foliage near the ends of branches.

Connecticut Warbler (*Oporornis agilis*).—A male netted by J. Dunning on 17 November 1979, in second growth bordering the lodge clearing, represents the first documented occurrence of this species in Peru (LSUMZ 93669: testes minute; moderate body fat; 12.5 g; prepared by T. S. Schulenberg). This species was known in South America from only a few localities in Colombia, Venezuela, and Brazil, where specimens were taken as close to southeastern Peru as the Río Madeira (Meyer de Schauensee 1966). It is probably overlooked throughout its winter range. Few other North American breeding passerines reach southern Peru as migrants or wintering birds; the following have been recorded on the reserve: Eastern Kingbird (*Tyrannus tyrannus*), Eastern Wood Pewee (*Contopus virens*), Alder Flycatcher (*Empidonax alnorum*), Bank Swallow (*Riparia riparia*), Barn Swallow (*Hirundo rustica*), Gray-cheeked Thrush (*Catharus minimus*), Swainson's Thrush (*Catharus ustulatus*), *C. fuscescens*, Bobolink (*Dolichonyx oryzivorus*), Canada Warbler (*Wilsonia canadensis*), and Scarlet Tanager (*Piranga olivacea*).

Slate-colored Seedeater (*Sporophila schistacea*).—Small numbers of this seedeater were present in flowering *Guadua* bamboo within forest on the reserve from mid-August to late November 1980 (A. Van Den Berg, P.

Donahue, M. Robbins, pers. comms.), and again in late October 1981 (pers. obs.). A female (LSUMZ 98681: skull not pneumatized; ovary 4 × 3 mm; 13 g; iris brown; bill black; tarsi and feet dark olive) was collected 22 Nov. 1980 by M. Robbins. In both years several males were noted almost daily as they sang from exposed perches within or near the crowns of bamboo thickets 5–10 m above ground. Phonetically the unmelodious song is *bzzz-tititi-psit-psit-psit-psit-psit-psit*; several other variations of this are also uttered. Several singing males were also noted in flowering bamboo in lower montane forest about 3 road km northeast of Abra Divisoria, in the Cordillera Azul, Dpto. Huánuco from 7 August–4 September 1979 (pers. obs.; P. Donahue, V. Emanuel, pers. comms.). The occurrence of this rather enigmatic species seems to depend on the presence of flowering bamboo—thus, it probably wanders widely through much of its range. This is the first report of the Slate-colored Seedeater from Peru; there was but one previous record of *S. schistacea* from south of Ecuador (Dpto. Beni, northern Bolivia [Meyer de Schauensee 1966]).

SUMMARY

Information on behavior, distribution, and taxonomy is presented for 36 species of lowland forest and marsh birds of southeastern Peru. Specimen data are given for the poorly known species. The first Peruvian records of *Chauna torquata*, *Porphyrula flavirostris*, *Coccyzus cinereus*, *Synallaxis albescens*, *Myrmotherula iheringi*, *Myiozetetes cayanensis*, *Catharus fuscescens*, and *Oporornis agilis* are reported. *Simoxenops ucayalae*, *Myrmeciza goeldii*, and *Poecilotriccus albifacies*, all known from fewer than 10 specimens, are discussed. The antbird *Percnostola macrolopha* Berlioz is shown to be the male of *P. lophotes*. A variety of resident species, including *Drymophila devillei* and *Ramphotrigon megacephala*, are found to be intimately associated with bamboo thickets. Finally, a small component of the avifauna, including *Coccyzus cinereus*, *Satrapa icterophrys*, *Casiornis rufa*, *Pseudocolopteryx acutipennis*, *Inezia inornata*, and *Turdus amaurochalinus*, is comprised of austral migrants.

ACKNOWLEDGMENTS

Several other people spent considerable amonts of time on the Tambopata Reserve, and they, too, have observed most of the birds reported herein. Paul Donahue has been especially dedicated to obtaining information on the avifauna of the region. Others who deserve special mention in this regard are Robert Ridgely, Mark Robbins, Thomas Schulenberg, and Bruce Sorrie. I thank J. V. Remsen, Jr., R. S. Ridgely, T. S. Schulenberg, and J. P. O'Neill for their careful reviews of this manuscript. The owners of the Explorer's Inn graciously allowed me and numerous other biologists to carry out studies on their property and offered a variety of assistance. I also gratefully acknowledge the continuing support of the Direccion General Forestal y de Fauna, Ministerio de Agricultura, Lima, Peru. Finally, I am greatly indebted to John S. McIlhenny, Babette M. Odom, Laura Schweppe, H. Irving Schweppe, and E. W. Mudge for their financial support of LSUMZ fieldwork.

LITERATURE CITED

Berlioz, J. 1966. Descriptions de deux especes nouvelles d'oiseaux de Pérou. Oiseau 36: 1–3.

Blake, E. R. 1959. A new species of *Todirostrum* from Peru. Nat. Hist. Misc. 171:1–2.

Fitzpatrick, J. W. 1979. Foraging behavior of Neotropical tyrant flycatchers. Condor 82: 43–57.

Forshaw, J. M. 1978. Parrots of the world. 2nd ed. Lansdowne Editions, Melbourne, Australia.

Gyldenstolpe, N. 1945a. The bird fauna of the Rio Juruá in western Brazil. Kungl. Sv. Vet. Akad. Handl. 22, No. 1.

———. 1945b. The ornithology of northern Bolivia. Kungl. Sv. Vet. Akad. Handl. 23, No. 1.

———. 1951. The ornithology of the Rio Purús region in western Brazil. Ark. Zool. Ser. 2, Bd. 2, No. 1.

Hellmayr, C. E. and J. von Seilern. 1914. Neue Vogel aus deur tropischen Amerika. Verh. Orn. Ges. Bayern 12:87–92.

Meyer de Schauensee, R. M. 1966. The species of birds of South America and their distribution. Livingston, Narberth, Pennsylvania.

———. 1970. A guide to the birds of South America. Livingston Publ. Co., Wynnewood, Pennsylvania.

Munn, C. A. and J. W. Terborgh. 1979. Multi-species territoriality in neotropical foraging flocks. Condor 81:338–347.

Norton, D. W. 1965. Notes on some non-passerine birds from eastern Ecuador. Breviora 230:1–11.

O'Neill, J. P. 1969. Distributional notes on the birds of Perú, including twelve species previously unreported from the republic. Occ. Pap. Mus. Zool., Louisiana State Univ. 37:1–11.

———. 1974. The birds of Balta, a Peruvian dry tropical forest locality, with an analysis of their origins and ecological relationships. Ph.D. diss., Louisiana State Univ., Baton Rouge, Louisiana.

——— and D. L. Pearson. 1974. Estudio preliminar de las aves de Yarinacocha, Depto. de Loreto, Perú. Publ. Mus. Hist. Natur. "Javier Prado," Ser. A. Zool. No. 25:1–13.

Parker, T. A., III and J. P. O'Neill. 1980. Notes on little-known birds of the upper Urubamba valley, southern Peru. Auk 97:167–176.

Pearson, D. L. 1975. Range extensions and new records for bird species in Ecuador, Peru and Bolivia. Condor 77:96–99.

Peters, J. L. 1951. Check-list of birds of the world. Harvard Univ. Press, Cambridge, Massachusetts.

Remsen, J. V., Jr. and R. S. Ridgely. 1980. Additions to the avifauna of Bolivia. Condor 82:69–75.

Short, L. L., Jr. 1969. A new species of blackbird (*Agelaius*) from Peru. Occ. Pap. Mus. Zool., Louisiana State Univ. 37:1–8.

———. 1975. A zoogeographic analysis of the South American Chaco avifauna. Bull. Am. Mus. Nat. Hist. 154:163–352.

Tallman, D., E. Tallman, and D. L. Pearson. 1977. The birds of Limoncocha, Napo Province, Ecuador. Instituto Linguistico de Verano, Quito 1–15.

Traylor, M. A., Jr. (ed.). 1979. Check-list of birds of the world. Harvard Univ. Press, Cambridge, Massachusetts.

Vaurie, C. 1980. Taxonomy and geographical distribution of the Furnariidae (Aves, Passeriformes). Bull. Am. Mus. Nat. Hist. 166.

MUSEUM OF ZOOLOGY, LOUISIANA STATE UNIV., BATON ROUGE, LOUISIANA 70893. ACCEPTED 5 MAY 1982.

Wilson Bull., 94(4), 1982, pp. 494–504

MIGRATION AND SUMMER DISTRIBUTION OF LESSER SNOW GEESE IN INTERIOR KEEWATIN

Peter L. McLaren and Margaret A. McLaren

Lesser Snow Goose (*Chen caerulescens caerulescens*) numbers have increased substantially over the last 30 years, especially at colonies in the eastern and central Arctic. The numbers of birds nesting at the west Hudson Bay colonies increased from an estimated 15,000 in 1955 (Cooch 1961) to 400,000 in 1973 (Kerbes 1975). Similarly, the nesting population at Cape Henrietta Maria, Ontario, has tripled since 1957, to about 50,000 birds in 1973 (Kerbes 1975). In the central Arctic, the Queen Maud Gulf population expanded from about 8400 nesters in 1965 (Ryder 1971) to 50,000 in 1977 (Kerbes, unpubl. cited by Dzubin 1979). Palmer (1976) identified the Baker Lake, Keewatin District, area as a major breeding area. However, there is only one record of 15 pairs nesting south of Baker Lake (Miller 1972).

Migration routes of Snow Geese in southern Canada and the United States are well documented (Bellrose 1976, Palmer 1976) but those over northern Canada are poorly understood. Eastern Arctic Snow Geese (Hudson Bay, Baffin Island) are believed to follow the coastlines of Hudson and James bays (Cooch 1961, Blokpoel 1974, Bellrose 1976); central Arctic Snow Geese (Queen Maud Gulf) are thought to arrive directly from and return directly to staging areas in northern Saskatchewan (Bellrose 1976, Palmer 1976). Palmer (1976), however, indicated the possibility of a route between Queen Maud Gulf and Hudson Bay. Dzubin (1979) believed that at least part of the increase of the central Arctic population was a result of immigration from the west Hudson Bay colonies along such a pathway. This belief was based on an increase in the proportion of blue morph geese in the central Arctic from 5% in 1966–1968 (Ryder 1971) to 15% in 1976 (Kerbes, unpubl. cited by Dzubin 1979); the latter value is much closer to the 24% figure at the west Hudson Bay colonies (Kerbes 1975). Dzubin, (1979), however, did not provide direct evidence of such a pathway.

Aerial surveys in Keewatin District, Northwest Territories, in 1975–1977 provided much new information on the distribution and movements of Lesser Snow Geese. This paper documents the 1975–1977 status of Lesser Snow Geese in northern Keewatin and the existence of previously unreported migration routes through interior Keewatin, and relates these to the present dynamics of Snow Goose populations in Keewatin District.

METHODS

Aerial surveys were conducted either by helicopter or fixed-wing aircraft. For surveys of molting and nesting areas a Hughes 500 helicopter was flown at an altitude of 15 m and a ground speed of 80 km/h. For surveys during the post-breeding and migration periods, a Cessna 185 or Cessna 337 fixed-wing aircraft was flown at 30 m and 160 km/h. Surveys of spring migration consisted of north-south transect lines, ranging from 120 km inland at the Manitoba border to 300 km inland west of Baker Lake, flown once to several times in 1976 (total of 1712 km); a single line flown from near the mouth of the Tha-anne River northwest to Henik Lake (160 km); and several lines flown in June 1976 in the Baker Lake–Pitz Lake area (370 km) (Fig. 1a). Surveys to record post-breeding dispersal in late summer in southern Keewatin consisted of a series of parallel lines from the Maguse to the Thlewiaza rivers flown twice in late summer 1975 and four times in late summer 1976. Each line consisted of 6–12 transects, each about 16 km in length (total of 4111 km). Sightings along each transect were recorded separately. Surveys of autumn migration in 1976 consisted of five surveys along the south side of Baker Lake in the 14 August–20 September period (total of 334 km), plus one to three surveys (depending on location) of the same route from Baker Lake south to the Manitoba border that were flown in spring (1433 km) (Fig. 1b).

Observers sat in the right front and left rear seats of the aircraft. For each sighting the observer dictated (into a tape recorder) the number of individuals and, except during nesting and molting surveys, whether the birds were within 200 m of the transect center-line. In this paper, many of the results are simply the flock sizes observed. However, results of surveys of the post-breeding movements in southern Keewatin are expressed as densities (number of geese/km^2) based on a total transect width of 400 m (200 m on each side of the aircraft). Densities reported are a simple extrapolation based on the total transect area. No correction factors have been applied.

RESULTS

Spring migration, southern and central Keewatin.—A total of 5451 Snow Geese in 19 flocks was recorded in interior southern Keewatin in spring 1976 (Fig. 1a). Flocks seen east of Yathkyed Lake and southeast of the Henik Lakes were flying north; most of those in the Baker Lake area were on the ground. In addition, we saw a flock of 1200 Snow Geese flying north over the Caribou River in extreme northern Manitoba, 50 km inland from the coast of Hudson Bay, on 22 May; and several flocks were seen passing north over the town of Baker Lake on 8–10 June.

Nesting and molting areas, central and northern Keewatin.—Although the major colonies in southern Keewatin are along the west coast of Hudson Bay, geese also nest at several locations inland (Clarke 1940, Miller 1972). During surveys between Pitz and Baker lakes in 1977, we found single nests and colonies totalling 139 nests, and 16 flocks containing a total of at least 47 young. In 1975 we located 76 nests and four flocks containing 99 young.

In early July 1975, we counted 543 nests and 3742 molters at four sites in the Rasmussen Basin lowlands of northern Keewatin (Fig. 2). Of 4832

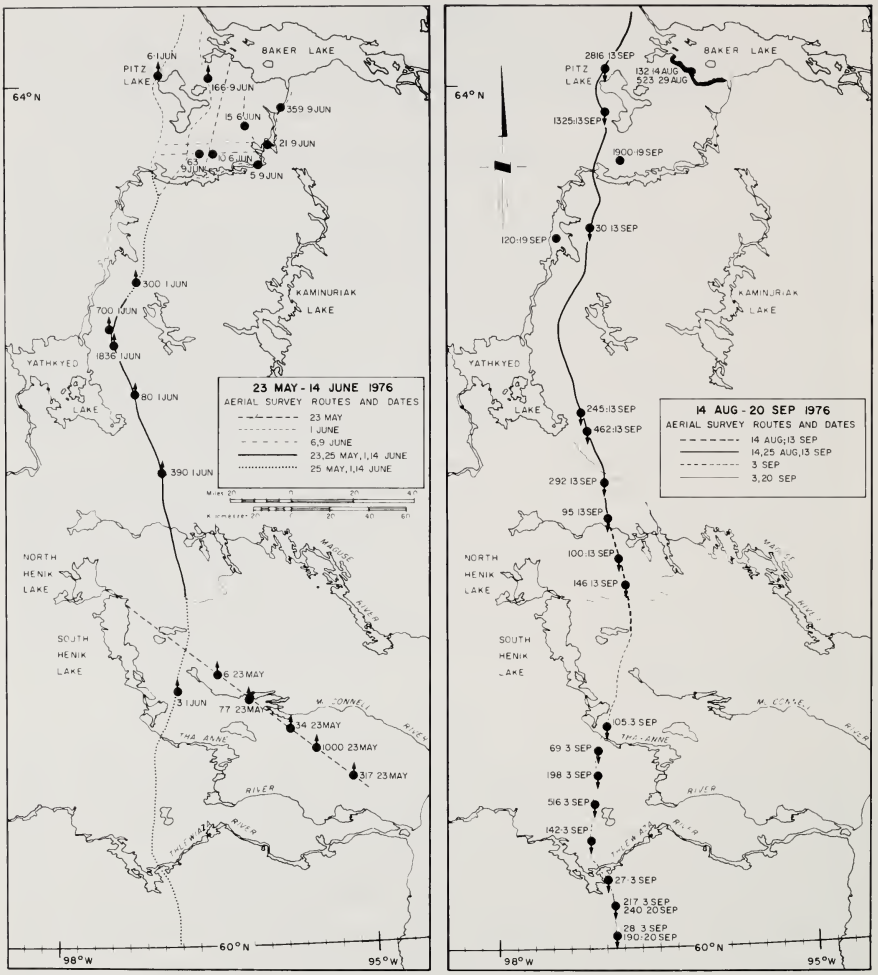


FIG. 1. Lesser Snow Goose sightings in southern Keewatin District, 23 May–14 June 1976 (Fig. 1a) and 14 August–20 September 1976 (Fig. 1b). Numbers indicate number of geese seen and date. Dark circle indicates location of flock and arrow indicates direction of flight.

nesting and molting geese classified, 21.7% were blue phase. Spring thaw was late in 1976; about 4800 molting Snow Geese but only 10 nests (nine at the colonies) and 15 broods were found in the Rasmussen Basin lowlands that year. In early July 1977, over 300 nests and 3772 molting birds were estimated from a photographic record of the colony sites. Of 927 geese classified from photographs, 21.9% were blue phase.

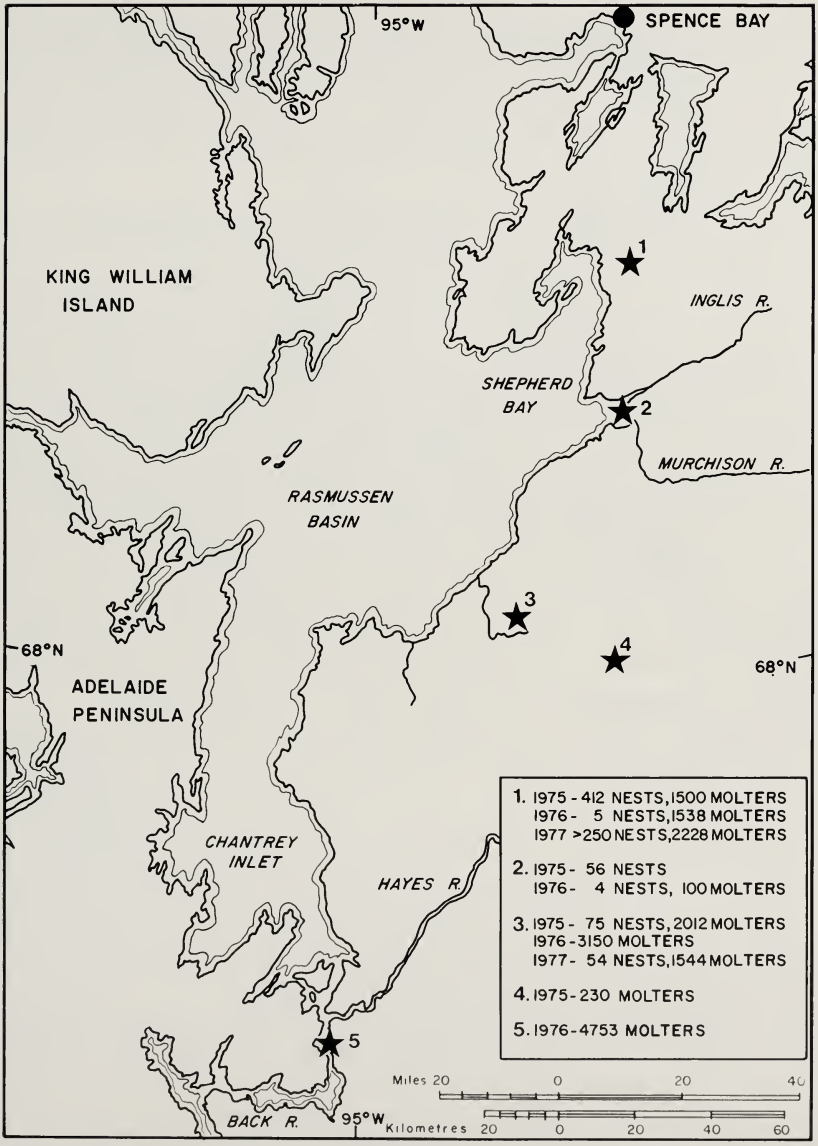


FIG. 2. Locations of nesting and molting Lesser Snow Geese in northern Keewatin District, 1975–1976.

We did not find a nesting colony at the mouth of the Back River but we did observe recently fledged young among the 717 Snow Geese recorded there in late August 1975, and three broods in early July 1976 when little nesting occurred in northern Keewatin. We also recorded 4753 molting Snow Geese in this area in early July 1976 but no estimate of the proportion of blue morphs was made (Fig. 2).

Post-nesting dispersal, southern Keewatin.—The main portion of the west Hudson Bay colonies is located along the coast between the mouths of the Maguse and Thlewiaza rivers (Kerbes 1975). We did not survey coastal areas, where many geese remain throughout the brood-rearing period, but we found that, as the summer progressed, many Snow Geese, including family groups, moved inland from these colonies. On 15 August 1976, the young were not yet able to fly and all young-of-the-year seen were along the lines 8 km and 24 km inland from these colonies. Older geese were present up to at least 72 km inland. During each subsequent survey, the number of geese 8 km inland became proportionately smaller and the numbers farther inland proportionately larger (Fig. 3, Table 1). Both adults and young-of-the-year were seen throughout the area after 15 August. By then the young could fly, but it is uncertain whether they flew or walked inland. The timing of the movement was apparently similar in 1975 when densities on 28 August were highest on the lines from 48–96 km inland and lowest on the line 8 km from the coast (Table 1).

In late August many of the 1.3 million Snow Geese from the west Hudson Bay colonies (Kerbes 1975) are in interior Keewatin. In late August 1976, we counted 4467 Snow Geese on the transect strips and an additional 12,000 beyond the edge of the transect. The transect strips covered only 2% of the area surveyed; simple extrapolation would indicate that 225,000 Snow Geese were in the area up to 120 km inland between the Thlewiaza and Maguse rivers. Although confidence limits cannot be placed on this estimate, the fact that 73% of the geese seen were beyond the transect strip suggests that the estimates are not unrealistic.

Autumn migration, central and southern Keewatin.—Results of the late summer surveys conducted around Baker Lake and south from the Baker Lake–Pitz Lake area to 60°N are shown in Fig. 1b. Numbers of Snow Geese seen along the southwest shore of Baker Lake increased in late August, to a maximum of 523 on 29 August. Other than on the surveys inland from the west Hudson Bay colonies (see above), Snow Geese were not seen south of Baker Lake during two surveys in August, but were present in the 3–20 September period (Fig. 1b). The geese in interior southern Keewatin on 3 September may have come from the coastal colonies 125+ km to the east as part of the inland dispersal described above. However, several large flocks (most notably 1900 Snow Geese near Pitz Lake on 19 September) were seen north of the Maguse River on 13 and

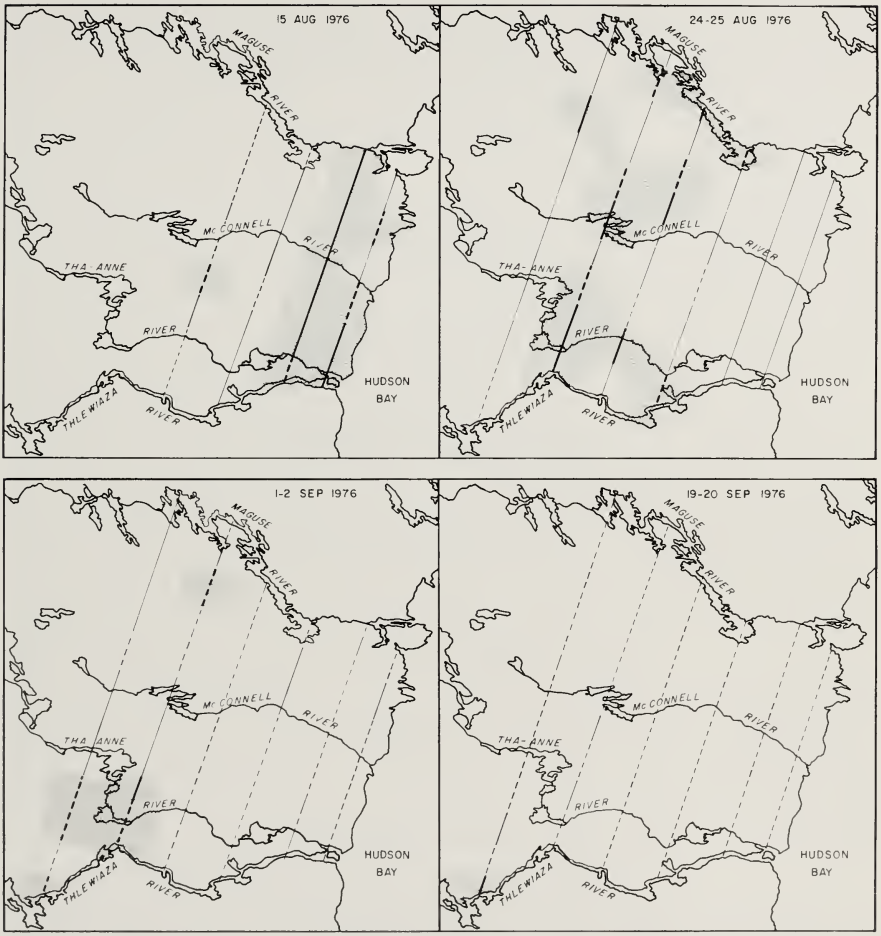


FIG. 3. Distribution of Lesser Snow Geese in southern Keewatin District, 15 August–20 September 1976. – – –: 0 geese/km²; ———: 1–20 geese/km²; – – –: 20–40 geese/km²; ———: 40+ geese/km². Shaded areas denote approximate areas with densities of greater than 20 geese/km². The areas shown are approximately 60°N to 62°N and 92°W to 97°30′W.

19 September. The latter date is considerably later than the peak of dispersal of geese inland from the west Hudson Bay colonies, and Pitz Lake is 340 km NNW of the northernmost west Hudson Bay colony.

DISCUSSION

Many of the recently observed changes in Snow Goose migration, e.g., the appearance of blue phase geese in Saskatchewan (Dzubin 1979), as well as changes in color-phase ratios at some colonies (Cooke et al. 1975),

Table 1

Numbers and Densities of Snow Geese between the Maguse and Thlewiaza Rivers in Late Summer of 1975 and 1976

Distance from Hudson Bay	23 July 1975		28 Aug. 1975		15 Aug. 1976		24–25 Aug. 1976		1–2 Sept. 1976		19–20 Sept. 1976	
	No.[a]	No./km²	No.	No./km²	No.	No./km²	No.	No./km²	No.	No./km²	No.	No./km²
8 km	—[b]	—	111	2.8	1400	37.0	108	2.9	6	0.2	0	0.0
24 km	2620	55.0	415	7.3	3591	81.5	192	4.4	10	0.2	0	0.0
48 km	14	0.3	1622	33.4	130	2.6	629	12.8	7	0.1	0	0.0
72 km	6	0.1	2034	37.6	194	3.6	1054	19.4	64	1.2	0	0.0
96 km	—	—	1990	32.5	—	—	1777	28.9	925	15.1	60	1.0
120 km	—	—	352	4.8	—	—	707	9.4	801	10.7	410	5.5

[a] Includes only birds seen "on transect."
[b] Indicates line not flown.

have occurred concurrently with the rapid increase in numbers of Snow Geese at the west Hudson Bay colonies. In this paper we present data that show probable changes in Snow Goose distribution, including apparently new migration routes through interior Keewatin in both spring and fall, the presence of new colonies, and extensive inland dispersal from the west Hudson Bay colonies.

Inland migration.—Data from our spring surveys in 1975 and 1976 suggest that many Snow Geese summering in the Keewatin District migrate through inland Keewatin rather than along the Hudson Bay coast. This inland movement also occurred in 1977 when Allen and Hogg (1978) saw 6100 Snow Geese east of Yathkyed Lake on 30 May. The destination of these geese is unknown but the Rasmussen Basin–Chantrey Inlet and/or the Queen Maud Gulf areas seem likely.

Similarly, Snow Geese seen near Baker Lake and Pitz Lake from late August to mid-September 1976 probably came from one or both of these areas. Snow melt and nest initiation were probably late in Queen Maud Gulf in 1976. (June temperatures at Cambridge Bay, the nearest weather station, were 2°C below normal.) If nest initiations peaked about 15 June, as they did in another late spring (Ryder 1971), most young would have fledged in late August–early September. Thus, adults and young could well have been in central Keewatin by mid-September.

Movements through inland Keewatin (as well as the westward dispersal from the west Hudson Bay colonies) are consistent with observed westward shifts in migration corridors farther south. Blokpoel (1974), and Blokpoel and Gauthier (1975) documented a westward shift of spring migration staging areas in southern Manitoba, and Dzubin (1979) documented increasing numbers of blue-phase geese (presumably originating from west Hudson Bay colonies) at Saskatchewan staging areas in fall.

Blokpoel (1974) documented departure directions for Snow Geese leaving southern Manitoba in spring. He assumed that all eventually intersected the Hudson Bay coast, but some of his reported tracks were toward interior Keewatin, not Hudson Bay. Whether Snow Geese were, in fact, migrating over interior Keewatin in 1970–71, when Blokpoel's study was conducted, is unknown. We have been unable to find any records prior to our own of Snow Geese migrating through inland Keewatin in the spring.

Dzubin (1979) postulated that 60,000 Snow Geese from the Queen Maud Gulf area migrate southeast to the coast of Hudson Bay and there join southward migrating geese from the west Hudson Bay colonies. Dzubin based his hypothesis on the disjunct distribution of band recoveries from southern Canada and the northern United States but had no direct evidence of such a corridor (Dzubin, pers. comm.). (Melinchuk and Ryder [1980], however, reported a direct recovery along the southern Hudson

Bay coast, of a Ross' Goose [*Chen rossii*] banded near Queen Maud Gulf.) While we have no data to disprove the existence of a corridor reaching to the coast of Hudson Bay, our data do suggest that many geese moving south from northern Keewatin remain well inland.

Rasmussen Basin, Chantrey Inlet Snow Geese.—We believe that the Snow Goose population in the Rasmussen Basin lowlands and probably that at the mouth of the Back River (Chantrey Inlet) are derived from the west Hudson Bay colonies. The presence of Snow Geese in both areas is apparently a recent phenomenon. Neither Bellrose (1976) nor Palmer (1976) included these areas in the breeding range of the Snow Goose; J. P. Ryder (pers. comm.) observed no Snow Geese at the mouth of the Back River in 1968. Both of these areas have thus been colonized recently, perhaps originally by molt migrants. In early July 1975, we found approximately three molting geese for every nesting goose in the Rasmussen Basin lowlands. The molting geese seen so early in the summer presumably were primarily pre-breeders, which begin to molt about 2.5 weeks earlier than breeding adults (Cooch 1958).

Abraham (1980) has documented the existence of molt migrations of non-breeding Lesser Snow Geese from the La Pérouse Bay (Manitoba) colony to the McConnell River area. Brace et al. (1978) suggested that non-breeders from the McConnell River colony migrate to other areas to molt. The Rasmussen Basin lowlands may be such an area. Prevett (pp. 139 *in* Palmer 1976) reported that small flocks of yearlings continued to overfly the McConnell River colony in a northerly direction in 1970 for several days after nesting birds had arrived at the colony. Birds that molt in the Rasmussen Basin lowlands as pre-breeders may return there to form the nucleus of the relatively small breeding colonies.

The phase ratio of geese in the Rasmussen Basin lowlands (22% blue geese in both 1975 and 1977) is similar to both the 24% blue geese along west Hudson Bay and the 23% blue geese on SW Southampton Island (Kerbes 1975). Proximity, possible introduction via molt migration, and population increases at west Hudson Bay colonies suggest that area as the most likely source of the Rasmussen geese. It is less likely that Rasmussen geese are derived from Queen Maud Gulf colonies since only 15% of the geese there are blue phase (Kerbes, unpubl. cited in Dzubin 1979).

Inland dispersal from west Hudson Bay colonies.—The dispersal of post-nesting geese inland from west Hudson Bay may be a response to feeding pressures on the coastal sedge meadows. Cooch (1958) observed brood-flock movements of up to 50 km on Baffin Island and suggested that such movements occurred in response to competition for limited sedge resources. Kerbes (1982) suggested that over-grazing at west Hudson Bay nesting areas may cause geese to move inland.

Geese with broods had moved on foot up to 24 km inland from Hudson Bay, or about 10 km west of the western edge of the nesting areas, by mid-August. We estimated that on 28 August 1975, 225,000 Snow Geese were in interior Keewatin between the Maguse and Thlewiaza rivers. Most of these geese were 72 km inland. We have been unable to find previous reports of large numbers of Snow Geese this far inland and Dzubin (pers. comm.) states that Inuit who lived in the vicinity of Henik Lakes in the early 1960's were not aware of Snow Geese inland in late summer.

Most geese seen in southern Keewatin in late August and early September were probably from the west Hudson Bay colonies. Adults and young from Queen Maud Gulf, Rasmussen Basin or Southampton Island do not arrive in southern Keewatin until September, since fledging at these colonies occurs in late August (Cooch 1958, Ryder 1971). However, some of the geese were probably non-breeders which leave the central Arctic colonies in late August. Thus, interior southern Keewatin may represent a point of contact between geese from west Hudson Bay and from the central Arctic. Maintenance of this contact over the winter could then result in a distributional shift of west Hudson Bay birds away from that area to the Rasmussen Basin-Chantrey Inlet area and possibly Queen Maud Gulf.

SUMMARY

Previously unreported migration routes, molting areas, and post-nesting dispersal patterns of Lesser Snow Geese (*Chen c. caerulescens*) in interior Keewatin District, Northwest Territories, were documented by aerial surveys in 1975–1977. In late May and June 1976, over 6000 migrants were seen over inland areas between the Caribou River, Manitoba, and Baker Lake, N.W.T. These geese probably summer in the Baker Lake area (ca. 300 geese), the Rasmussen Basin-Chantrey Inlet area (ca. 10,000 geese), and possibly the Queen Maud Gulf. Substantial numbers of Snow Geese, including broods, from the colonies along western Hudson Bay disperse inland in late August, presumably to feed. The movement is initially on foot. In September, migrants from areas farther north pass southward through interior Keewatin. The present of large numbers of Snow Geese in the Rasmussen Basin-Chantrey Inlet area and in interior southern Keewatin, the inland dispersal from western Hudson Bay, and the use of inland migration routes are all recent developments, and are probably related to the very rapid increase in Snow Goose numbers and consequent increased feeding competition at the west Hudson Bay colonies.

ACKNOWLEDGMENTS

This work was part of a larger study undertaken by LGL Ltd., Toronto, Ontario, for the Polar Gas Project. Coordination of logistics was provided by A. B. Ross of Polar Gas. Surveys were conducted by the authors and by W. G. Alliston, R. A. Davis, D. Fidler, W. G. Johnston, L. A. Patterson, and W. E. Renaud of LGL Ltd. Assistance and guidance in analysis were provided by R. A. Davis, C. Holdsworth, and W. J. Richardson of LGL Ltd. J. Riddick of Polar Gas, R. A. Davis, and W. J. Richardson of LGL Ltd., A. Dzubin and R. Kerbes of the Canadian Wildlife Service, J. P. Ryder of Lakehead University, and K. F. Abraham of the University of Western Ontario reviewed early versions of the manuscript. B. DeLong prepared the figures.

LITERATURE CITED

Allen, D. L. and T. H. Hogg. 1978. Bird studies in the Keewatin District. Can. Wildl. Serv. ESCOM Rept. No. AI–27.

Abraham, K. 1980. Moult migration of Lesser Snow Geese. Wildfowl 31:89–93.

Bellrose, F. C. 1976. Ducks, geese and swans of North America. Stackpole Books, Harrisburg, Pennsylvania.

Blokpoel, H. 1974. Migration of Lesser Snow and Blue geese in spring across southern Manitoba. Pt. 1. Distribution, chronology, directions, numbers, heights and speeds. Can. Wildl. Serv. Rept. Ser. No. 28.

——— and M. C. Gauthier. 1975. Migration of Lesser Snow and Blue geese in spring across southern Manitoba. Pt. 2. Influence of weather and prediction of major flights. Can. Wildl. Serv. Rept. Ser. No. 32.

Brace, R. K., R. H. Kerbes, A. X. Dzubin, and G. W. Beyersbergen. 1978. International arctic Snow Goose study. Report to the Mississippi and Central Flyway Council Technical Sections in the 1977 pilot program. Can. Wildl. Serv. Rept., unpubl.

Clarke, C. D. H. 1940. A biological investigation of the Thelon Game Sanctuary. Natl. Mus. Can. Bull. 96.

Cooch, F. G. 1958. The breeding biology and management of the Blue Goose *Chen caerulescens*. Ph.D. thesis, Cornell Univ., Ithaca, New York.

———. 1961. Ecological aspects of the Blue-Snow Goose complex. Auk 78:72–89.

Cooke, F., C. D. MacInnes, and J. P. Prevett. 1975. Gene flow between breeding populations of Lesser Snow Geese. Auk 92:493–510.

Dzubin, A. 1979. Recent increases of Blue Geese in western North America. Pp. 141–175 *in* Management and biology of Pacific flyway geese (R. L. Jarvis and J. C. Bartonek, eds.). OSU Bookstores, Corvallis, Oregon.

Kerbes, R. H. 1975. Lesser Snow Geese in the Eastern Canadian Arctic. Can. Wildl. Serv. Rept. Ser. No. 35.

———. 1982. Lesser Snow Geese and their habitat on west Hudson Bay. Nat. Can. 109 (in press).

Melinchuk, R. and J. P. Ryder. 1980. The distribution, fall migration routes and survival of Ross's Geese. Wildfowl 31:161–171.

Miller, F. L. 1972. Birds nesting at Kazan Falls. Auk 89:183–185.

Palmer, R. S. (ed.). 1976. Handbook of North American birds. Vol. 2. Waterfowl. Yale Univ. Press, New Haven, Connecticut.

Ryder, J. P. 1971. Distribution and breeding biology of the Lesser Snow Goose in central Arctic Canada. Wildfowl 22:18–28.

LGL LTD., 414-44 EGLINTON AVE. W., TORONTO, ONTARIO M4R 1A1, CANADA. ACCEPTED 20 MAY 1982.

WILDLIFE CONFERENCE

The 7th Annual Dr. Barbara Sawyer Memorial Wildlife Conference will be held at the California Academy of Sciences in San Francisco, California, 5–6 February 1983. The conference theme is raptor rehabilitation and will include such topics as captive raptor husbandry, rehabilitation techniques, population dynamics, nutritional requirements, veterinary techniques, and captive propagation.

Registration information is available from San Francisco Zoological Society, Sloat Blvd. at the Pacific Ocean, San Francisco, California 94132.

Wilson Bull., 94(4), 1982, pp. 505–514

ECOLOGICAL SEPARATION OF GREBES AND COOTS: INTERFERENCE COMPETITION OR MICROHABITAT SELECTION?

Thomas D. Nudds

Interspecific competition is assumed to be an important organizing force in natural communities and, in particular, responsible for patterns of niche diversification among ecologically similar species. However, because species' differences in resource use may not be the product of interspecific competition in sympatry, but may evolve in allopatry, "first level" (Huey 1979) evidence for competition, i.e., description of niche differences, is ambiguous with respect to defining the role of competition in producing different resource use patterns among coexisting species. This possibility tends to render even "level two" evidence for competition, e.g., the demonstration of niche complementarity (high overlap in one resource dimension associated with low overlap in another) suspect (Huey 1979). Also, the degree of resolution of patterns of resource use (i.e., the "scale" of investigation—over macrohabitats or microhabitats) can lead to different conclusions with respect to the degree to which species are ecologically separated and the factors responsible (Wiens and Rotenberry 1979, Nudds 1980).

Faaborg (1976) studied macrohabitat separation of Horned (*Podiceps auritus*) and Pied-billed (*Podilymbus podiceps*) grebes over a large area in North Dakota that included more than 500 prairie potholes. He found that below a threshold size (7.3 ha), only one species of grebe occupied the pothole. On larger potholes, as many as three grebe species (including the Eared Grebe [*Podiceps caspicus*]) were found. Faaborg (1976:397) advanced several ideas to account for these observations. These can be combined into two major hypotheses. Faaborg invoked the "compression hypothesis" to account for the disjunct pond occupancy patterns of *auritus* and *podiceps* on small potholes. Following Wedemeyer (1932), he reasoned that diet overlap must be high among prairie nesting grebes due to the absence of fish from most wetlands which are used differentially by grebe species elsewhere (Wetmore 1924, Munro 1940) and that interspecific interference competition might maintain the "fairly complete division of these species by habitat." Second, on large potholes with more than one grebe species, he hypothesized a diversity-area effect. Grebe diversity was enhanced on those potholes because of increased habitat complexity that fulfilled the niche requirements of more species.

I examined these hypotheses and the ecological separation of members

of the *auritus-podiceps-Fulica americana* (American Coot) guild, by using data on macro- and microhabitat use collected on intensively studied potholes in the aspen-parkland of southwestern Manitoba. The species array is ecologically meaningful because coots and grebes apparently use potholes similarly for nesting and foraging (Ferguson 1977). I examined whether the disjunct occupancy patterns of small potholes observed at the macrohabitat level were the result of displacement via short-term competitive interactions or if the differential use of potholes similar at the macrohabitat level was the result of subtle differences in microhabitat use. I reasoned that if competition could account for the complementary distribution of Horned and Pied-billed grebes on similar-sized potholes (i.e., macrohabitat), then both macrohabitat and microhabitat separation would be small. On the other hand, if complementary species' distributions and large macrohabitat overlap were the result of subtle differences in species' microhabitat selection, then microhabitat separation would be large.

STUDY AREA AND METHODS

Data were collected during a study of community organization of breeding ducks from April–July 1978 (Nudds 1980). Nine potholes were selected from those on a 1.62-km² study area approximately 10 km NE of Minnedosa, Manitoba. The area was described by Dzubin (1969). Size and depth characteristics of each pothole varied (Table 1). Ponds A and I were temporary type 1 (Smith 1971), ponds B, C, E, and F were semipermanent type 3, and ponds D, G, and H were permanent type 5 potholes. All potholes held water throughout the study, but A and I were overgrown with emergent vegetation by 8 June. Pothole D was surrounded by a homogeneous cattail (*Typha latifolia*) stand, potholes C, F, G, and H by homogeneous bulrush (*Scirpus* sp.) stands, and the remaining potholes were surrounded by heterogeneous emergent vegetation associations that included those species and whitetop (*Fluminea festucacea*). Ponds A and I and the edges of some larger ponds supported a diverse group of floating and submerged plants, the most common being duckweeds (*Lemma* sp.), milfoil (*Myriophyllum exalbescens*), crowfoot (*Ranunculus subrigidus*), hornwort (*Ceratophyllum demersum*), bladderwort (*Utricularia vulgaris*), and pondweeds (*Potamogeton* spp.). The large green alga, *Chara* sp., was abundant in ponds G and H and a smaller filamentous alga was abundant in pond E.

The perimeters of each of the nine study ponds were marked at 10-m intervals with color-coded 2-m × 2.5 × 5.0-cm wooden stakes before birds arrived in the spring. The coordinates of the grids (Fig. 1) were numbered and features of microhabitat structure were measured at each. Water depth was measured between 26 April and 1 May, and 16–23 May. Average depth for a quadrat was obtained from measurements at the four grid-points which delineated it. Three structural aspects (one vertical, two horizontal) of the vegetation and vegetation height were measured. The profile of the emergent vegetation was measured at each grid-point using a profile board modified after Nudds (1977). Quintile scores (1–5) for percent vegetation cover of the board at each of four heights (0.25, 0.5, 1.0, and 1.5 m) were estimated, converted to proportions of total vegetation, and substituted into $1/\Sigma p_i^2$. The mean of four values of each variable recorded determined the values for each quadrat. The proportions of the total area of each quadrat that were composed of dry, upland vegetation (usually grass), emergent vegetation, and open water were used as one index of horizontal

TABLE 1
SIZE AND DEPTH CHARACTERISTICS OF NINE POTHOLES AT MINNEDOSA, MANITOBA

Pond	Size (ha)	Depth (cm) $\bar{x} \pm SD$
A	0.15	29.0 ± 3.5
B	0.87	84.8 ± 14.6
C	0.92	34.0 ± 1.7
D	0.82	78.9 ± 19.6
E	1.04	36.5 ± 19.6
F	1.71	63.8 ± 12.4
G	0.48	76.8 ± 21.3
H	0.30	101.0 ± 32.5
I	0.36	33.3 ± 7.4

microhabitat complexity. A second measure was derived by counting the number of "islands" (patchily distributed clumps) of emergent vegetation in three size categories (<0.3 m, >0.3 m but <1 m, and >1 m in diameter) in each quadrat. Island-size diversity was calculated as above. Vegetation data were collected between 16 and 23 May.

Observations on habitat use by coots and grebes were conducted from blinds entered before sunrise to minimize disturbance. Two observers rotated among the blinds to minimize the introduction of directional bias and enhance the amount of data collected. Observations were made on 62 days between 26 April and 9 July with spotting scopes and binoculars. Observers recorded the species and location of individual coots and grebes on scale maps of each pothole (Fig. 1) at 0.5-h intervals for 4 h. Values of microhabitat characteristics for the quadrat in which an individual was recorded were assigned to that individual.

I used stepwise discriminant function analysis (DFA, Nie et al. 1970) preceded by principal component analysis (PCA, Nie et al. 1970) to delineate species' differences in microhabitat use and assign relative importance to those structural habitat features that maximally segregated species. PCA was performed to reduce the amount of redundant information contained in the matrix of intercorrelated habitat variables by producing a smaller number of orthogonal principal components (PC's) which were linear combinations of the original variables. Species' scores on the PC's were used as the orthogonal discriminating variables in DFA. This step is essential if the order in which a discriminating variable is selected in a stepwise procedure is to be interpreted as its relative importance as an ecological segregator of species (Green 1979).

RESULTS

Total hours of observation (N = 372.0) were distributed among the potholes as follows: A = 28.5, B = 48.0, C = 45.5, D = 51.0, E = 46.5, F = 43.0, G = 41.5, H = 41.5, and I = 26.5. Observations on potholes A and I were terminated on 8 June when vegetation growth prevented use by birds. The number of observations of each species were *auritus*, N = 180; *podiceps*, N = 101; and *americana*, N = 856. The distribution of observations of each species varied by pond (Fig. 2).

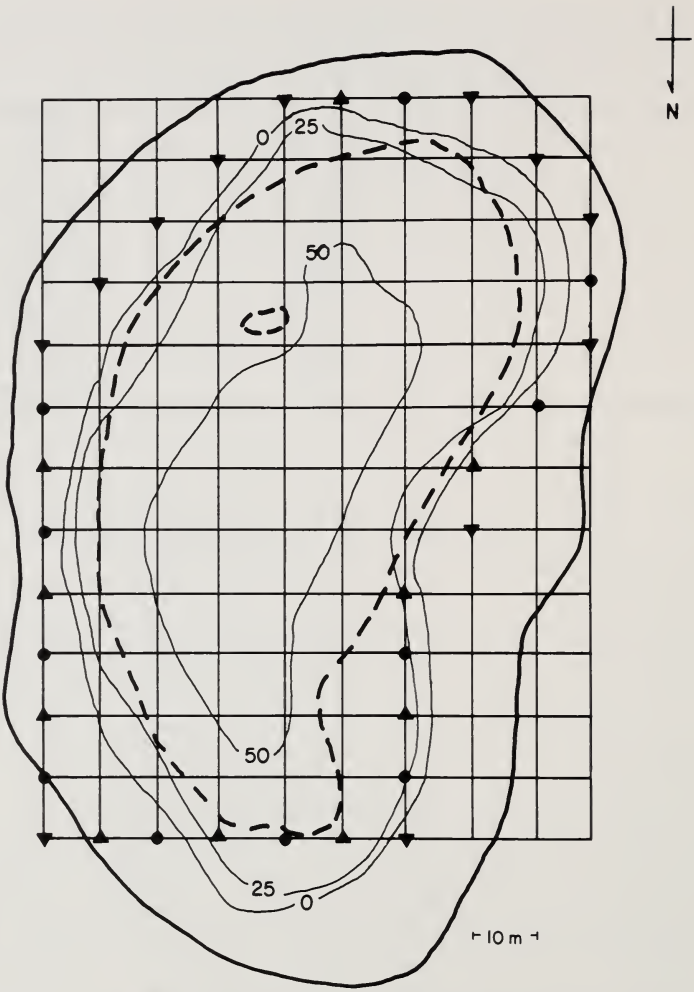


FIG. 1. Map of pond C with stakes outlining the grid.

None of the three species used pothole I; only *americana* fed (but did not nest) on pothole A. All three species fed and/or nested on the remaining seven potholes. Birds were not individually recognizable, but it was certain (because of territorial tenacity [Ferguson 1977]) that, with the exception of potholes G and H, all potholes were occupied by more than one pair of each species.

Macrohabitat use.—There was considerable macrohabitat overlap among species (i.e., with respect to gross pothole characteristics such as size,

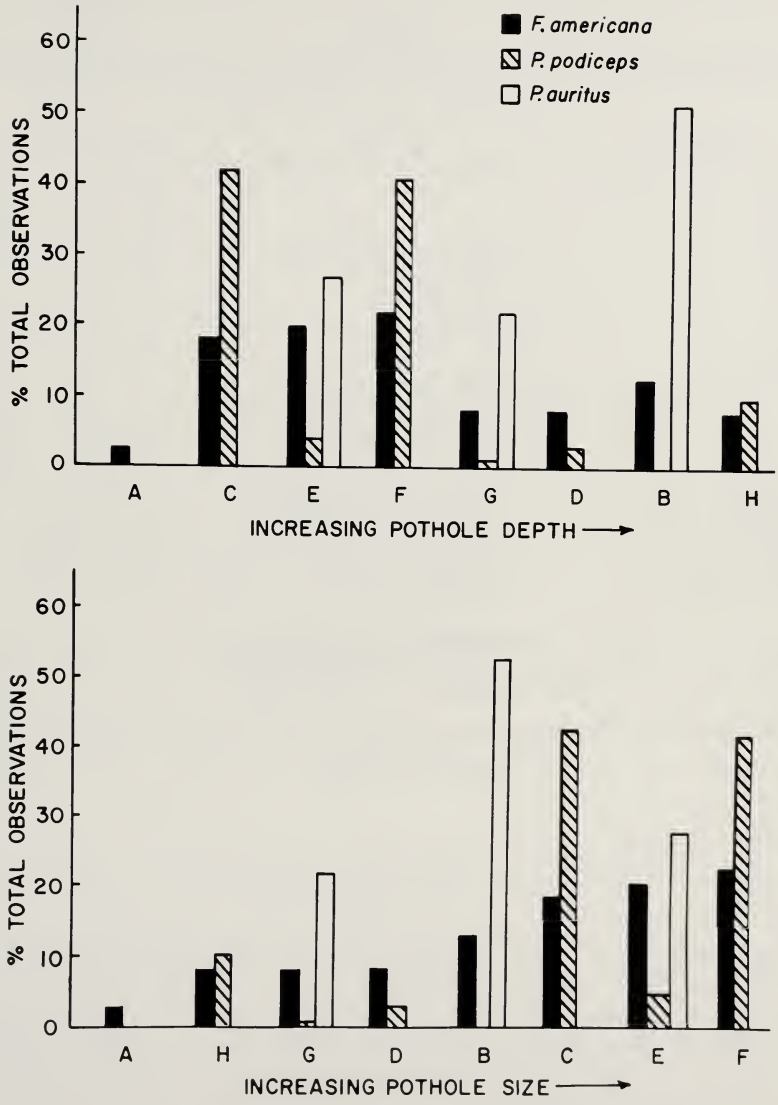


FIG. 2. Distribution of coots and grebes on pond depth and size gradients.

depth, and hence, permanence-type; Fig. 2). Coots were the most generalized species with respect to pothole use. Pied-billed Grebes tended to use shallow potholes surrounded by homogeneous stands of *Scirpus* (C and F); Horned Grebes used deeper potholes (G and B, but also E) with (G) or without (B and E) homogeneous stands of *Scirpus*. Pothole size was also an inadequate species' segregator (Fig. 2).

TABLE 2
MICROHABITAT FEATURES AND PRINCIPAL COMPONENT LOADINGS FOR THE GREBE-COOT GUILD AT MINNEDOSA, MANITOBA

Variable	Description	PC 1	PC 2
Depth	water depth	−0.75	
L1		0.91	
L2	vegetation density in each	0.94	
L3	of four layers	0.80	
L4	(see text)	—	
SUML	ΣL	0.94	
DIVERVEG	vertical complexity of vegetation (see text)	0.95	
VEGHGHT	vegetation height	0.88	
UPLAND	proportion of quadrat that	—	
EMERG	was upland or emergent	—	
WATER	vegetation or water	0.75	
DISPAVEG	spatial complexity of vegetation (see text)	0.87	
NA	number of 'islands' in each		—
NB	of three size categories (see		0.66
NC	text)		0.60
SUMN	number of 'islands'		0.73
DICLUMPS	'island-size' diversity		0.73
Cumulative % variance explained		70.4	

Two grebe species occurred on two of the seven potholes, even though all of the potholes were smaller than the 7.3-ha one-species threshold level identified by Faaborg (1976). Nevertheless, the almost complete complementarity of *auritus* and *podiceps* distributions is as Faaborg (1976) observed. Is this the result of competitive exclusion, or between-pond differences in microhabitats used by each species?

Microhabitat use.—Two independent microhabitat dimensions (Table 2) were identified by PCA and together accounted for >70% of the total variance among the original microhabitat variables. PC 1 described a continuum of microhabitat structure from deep, open water sites with no emergent vegetation to tall, dense, spatially uniform stands of emergent vegetation in shallow water. PC 2 was a gradient of spatial microhabitat complexity (vegetation interspersion, Table 2).

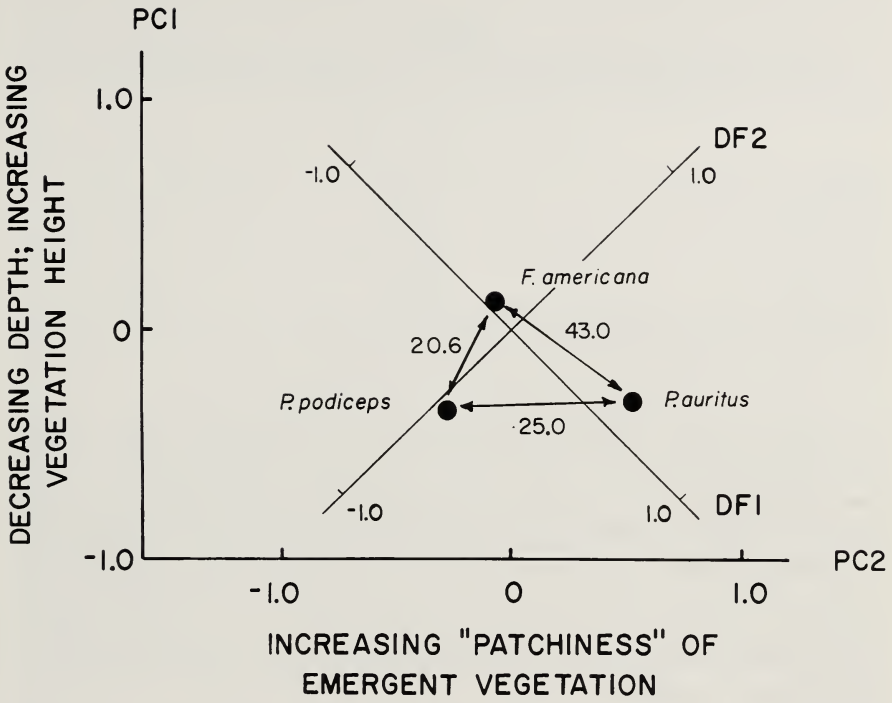


FIG. 3. Relation of coots and grebes in 2-dimensional microhabitat space and the discriminant axes along which the species are maximally segregated.

Coots occupied microhabitats with shallow water; grebes used deeper portions of ponds (Fig. 3). Pied-billed Grebes occurred in the densest emergent vegetation, *americana* was intermediate in that respect, and *auritus* used microhabitats with the greatest degree of water-vegetation interspersion (Fig. 3).

DFA identified PC 2 as the best ecological segregator of species. Microhabitat separation was large ($F = 34.53$, $P < 0.0001$), but species' pairwise niche separation varied from little separation between *americana* and *podiceps* to large separation between *americana* and *auritus* (Table 3). The two grebe species were highly separated in the vegetation interspersion dimension (Table 3). After entry of PC 1 in the discriminant model, overall species separation decreased but still differed markedly ($F = 31.24$, $P < 0.0001$). There was a greater degree of species' overlap in the depth dimension than in the spatial complexity dimension, which caused overall species' separation, and the pairwise separation of *amer-*

TABLE 3

MICROHABITAT SEPARATION[a] MATRICES IN ONE- (UPPER) AND TWO-DIMENSIONAL (LOWER) DISCRIMINANT SPACE FOR THE GREBE-COOT GUILD AT MINNEDOSA, MANITOBA

	F. americana	*P. podiceps*
P. podiceps	4.68	—
P. auritus	58.63	47.35
P. podiceps	20.58	—
P. auritus	43.02	25.03

[a] Maximum among-to-within species variance in microhabitat use.

icana-auritus and *podiceps-auritus* to decrease. However, the pairwise separation of *americana* and *podiceps* increased (Table 3). Thus, for the species-pair (*americana-podiceps*) occupying the most similar microhabitats with respect to vegetation interspersion, separation on the depth gradient was greatest. For the species pairs (*americana-auritus* and *podiceps-auritus*) that were largely separated on the gradient of vegetation interspersion, separation on the depth gradient was less. These results suggest complementarity of species' distributions along uncorrelated gradients of microhabitat structure.

DISCUSSION

There was considerable overlap in habitat use as measured by gross pothole characteristics such as size, depth, and permanance, but grebe species had largely complementary distributions over those macrohabitat gradients. Coots were generalists and used all types of wetlands (Sugden 1979). Grebe distributions can be explained without invoking competitive displacement via interspecific aggression. Grebe species used structurally different microhabitats; those microhabitats were differentially represented on potholes otherwise similar with respect to macrohabitat features.

Species' separation was greatest along a microhabitat structure gradient reflecting "patchiness" of emergent vegetation. *P. auritus* selected microhabitats with greater vegetation interspersion (Sugden 1977) an important aspect of nest placement by that species (Ferguson 1977). Conversely, *podiceps* selected microhabitats with dense emergent vegetation (Faaborg 1976, Glover 1953). Chabreck (1963), however, reported that breeding *podiceps* in Louisiana used microhabitats similar to those used by *auritus* in the prairies. The breeding range of *auritus* does not extend to Louisiana (Ferguson 1977) and the use of structural microhabitats there by *podiceps* may be an example of ecological release of *podiceps* into microhabitats

ordinarily used by *auritus*. That hypothesis assumes that exploitation competition in evolutionary time contributed to evolved species' differences in microhabitat use. Nevertheless, it is unnecessary to postulate that short-term interference competition between *auritus* and *podiceps* is responsible for their disjunct use of small ponds in the prairies.

Schoener (1975:248) postulated a continuum of mechanisms responsible for differential habitat use from behavioral (short-term) interference and displacement to genetic (innate habitat preferences). Grebes are divergent in habitat use (i.e., nearer the 'genetic' end of Schoener's continuum) and species' coexistence is enhanced by habitat complexity which fulfills the requirements of each species (Faaborg 1976). In this context, the significance of interspecific aggression as evidence that species compete for space is diminished and viewed as simple defense of, say, nesting platforms, which are attractive to conspecifics and other grebes, coots, and ducks as loafing sites (Ferguson 1977). Morris (1981) hypothesized that among organisms that are habitat selectors, most encounters will be with conspecifics, and occasional interspecific aggressive encounters may result because individuals behave to all other individuals as if they were conspecifics.

Lack of evidence of competition in the short-term does not mean that competition was unimportant in shaping observed species' differences in resource use. Competition may be periodically enhanced by depressed resource levels, particularly in variable environments like the prairies (Wiens 1977). It would be informative to follow the dynamics of species' habitat use over time for the grebe-coot guild through periods of resource depression and super-abundance.

SUMMARY

Faaborg (1976) studied macrohabitat separation of grebes on prairie potholes and postulated (1) that grebe diversity was related to an area-diversity effect on potholes greater than 7.3 ha, and (2) that the occurrence of single grebe species on potholes less than 7.3 ha was related to interspecific interference competition. A study of macro- and microhabitat use by coots and grebes revealed large overlap in macrohabitat use but significant differences in microhabitat use. Only one grebe species occupied small potholes because potholes differed with respect to the amount of vegetation-water interspersion used by each species; this results in disjunct species distributions. Presence of suitable microhabitat thus determines grebe diversity over all sizes of potholes, and it is unnecessary to postulate that short-term interference competition is responsible for single species occupancy of small potholes.

ACKNOWLEDGMENTS

I thank R. W. Cole, J. McA. Eadie, and L. G. Sugden for critical reviews of the manuscript. J. McA. Eadie and L. Nudds assisted with fieldwork. Financial assistance was provided through grants and/or contracts from the Canadian Wildlife Service, Department of Indian and Northern Affairs, Canadian National Sportsmen's Fund, and Natural Sciences and Engineering

Research Council of Canada support to C. D. Ankney. Time to analyze data and write the paper was provided through a Department of Environment Visiting Fellowship in Government Laboratories. I thank J. H. Patterson for his support in acquiring the fellowship. L. A. Tomkewich typed the paper.

LITERATURE CITED

CHABRECK, R. H. 1963. Breeding habits of the Pied-billed Grebe in an impounded coastal marsh in Louisiana. Auk 80:447–452.

DZUBIN, A. 1969. Assessing breeding populations of ducks by ground counts. Pp. 178–230 *in* Saskatoon wetlands seminar, Can. Wildl. Serv. Rept. Ser. No. 6.

FAABORG, J. 1976. Habitat selection and territorial behavior of the small grebes of North Dakota. Wilson Bull. 88:390–399.

FERGUSON, R. S. 1977. Adaptations on the Horned Grebe for breeding in prairie pothole marshes. M.Sc. thesis, Univ. Manitoba, Winnipeg, Manitoba.

GLOVER, F. A. 1953. Nesting ecology of the Pied-billed Grebe in north-eastern Iowa. Wilson Bull. 65:32–39.

GREEN, R. H. 1979. Sampling design and statistical methods for environmental biologists. Wiley, New York, New York.

HUEY, R. B. 1979. Parapatry and sympatry in the complementarity of Peruvian Desert Geckos (Phyllodoctylus): the ambiguous role of competition. Oecologia 34:249–259.

MORRIS, D. W. 1981. The pattern and structure of habitat utilization in temperate small mammals. Ph.D. thesis, Univ. Calgary, Calgary, Alberta.

MUNRO, J. A. 1940. The grebes. Studies of waterfowl in British Columbia. B.C. Prov. Mus. Occ. Pap. 3.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT. 1970. Statistical package for the social sciences. McGraw-Hill, New York, New York.

NUDDS, T. D. 1977. Quantifying the vegetative structure of wildlife cover. Wildl. Soc. Bull. 5:113–117.

———. 1980. Resource variability, competition, and the structure of waterfowl communities. Ph.D. thesis, Univ. Western Ontario, London, Ontario.

SCHOENER, T. W. 1975. Presence and absence of habitat shift in some widespread lizard species. Ecol. Monogr. 45:233–258.

SMITH, A. B. 1971. Ecological factors affecting waterfowl production in the Alberta parklands. U.S. Bur. Sport Fisheries and Wildl. Resource Publ. No. 98.

SUGDEN, L. G. 1977. Horned Grebe breeding habitat in Saskatchewan parklands. Can. Field-Nat. 91:372–376.

———. 1979. Habitat use by nesting American Coots in Saskatchewan parklands. Wilson Bull. 91:599–607.

WEDMEYER, W. 1932. Notes on the food of grebes. Auk 49:456.

WETMORE, A. 1924. Food and economic relations of North American grebes. U.S. Dept. Agric. Bull. 1196.

WIENS, J. A. 1977. On competition and variable environments. Am. Scient. 65:590–597.

——— AND J. T. ROTENBERRY. 1979. Diet niche relationships among North American grassland and shrub-steppe birds. Oecologia 42:253–292.

CANADIAN WILDLIFE SERVICE, PRAIRIE MIGRATORY BIRD RESEARCH CENTRE, 115 PERIMETER RD., SASKATOON, SASKATCHEWAN S7N 0X4 CANADA. (PRESENT ADDRESS: DEPT. ZOOLOGY, UNIV. GUELPH, GUELPH, ONTARIO N1G 2W1, CANADA.) ACCEPTED 10 FEB. 1982.

Wilson Bull., 94(4), 1982, pp. 515–530

ROLE SPECIALIZATION IN THE PARENTAL AND TERRITORIAL BEHAVIOR OF THE KILLDEER

John T. Mundahl

Variability in the role structure and mating systems of Charadriiformes has been extensively documented (Jenni 1974, Pitelka et al. 1974, Hildén 1975). Several papers have discussed the adaptive significance of these social systems, especially in regard to the behavioral mechanisms involved (Oring and Knudson 1972, Parmelee and Payne 1973, Graul 1974, Pitelka et al. 1974, Emlen and Oring 1977, Graul et al. 1977, Jenni and Betts 1978, Oring and Maxson 1978). Some of the latter have addressed the theoretical role of parental investment (see Trivers 1972) in explaining the ecological significance of a given mating system (Graul 1974, Emlen and Oring 1977, Graul et al. 1977). As noted by Pierotti (1981) many aspects of parental investment (as defined by Trivers 1972) are difficult or impossible to quantify. However, Pierotti (1981) and Burger (1981) quantify aspects of "parental care" for the Western Gull (*Larus occidentalis*) and the Black Skimmer (*Rynchops niger*), relating sex role patterns in parental care to the reproductive and ecological "strategies" of these species. Such is the objective of this paper, with the Killdeer (*Charadrius vociferus*) serving as the model.

STUDY AREA AND METHODS

This study was conducted during March–July 1975, May–June 1976, and from March–May 1977. The study site, approximately 4 km west of Logan, Cache Co., Utah, and 3 km east of the Little Bear River on State Highway 69, consisted of adjacent, grazed pastures of 1.15 ha and 0.18 ha, respectively.

Observations were made daily for 5 h beginning 30 min after sunrise in 1975. Observations were not made daily in 1976 and 1977 but the same temporal schedule was followed. Total observation time exceeded 400 h over the three breeding seasons. Killdeers were watched from an automobile with 7 × 35 binoculars and a 20× spotting scope at distances of less than 75 m. Behavior of the birds was monitored; behavioral units of previous workers are cited in the text and other behaviors are described as follows: The "flight chase" consisted of an aerial approach resulting in displacement of a conspecific. In the "killdeer display" the displaying bird lowered its head and pointed its bill downward; vocalizing was variable but repetitive "killdeer calling" (60–80 times per min) was always included. In the "stand off/parallel run" chasing occurred as in the "ground chase" (Phillips 1972:3–4, Fig. 2a, b, d) although no bird was clearly dominant and participants might change positions (Bunni 1959:240–244, 245). In the "preen" the subject preened in a fluffed, oblique position often orienting the cinnamon rump and back toward other birds; preening motions were quick, cursory and abbreviated. This display/comfort activity was performed on hummocks or other high places in the territory. "*Deet* calling" employed the *deet* vocalization (20–25 syllables per min). Bunni (1959) and Bursian (1971) considered this vocalization a contact call. In the

Table 1

Hours of Observation of Male and Female Killdeers at Different Stages of Reproduction[a]

Stage[b]	Males	Females	χ^2
PN	42	38	0.20
EL	29	17	3.13
I	51	46	0.26
B	10	11	0.05
Total	132	112	1.64

[a] Values were omitted for nests where the female deserted the brood after hatching. None of the observed differences between males and females was significant (χ^2 test, $P > 0.05$).

[b] PN = prenesting period; EL = egg-laying period; I = incubation period; B = brooding period.

"stand/rest" the subject stood fluffed on a hummock for more than 10 min neither vocalizing nor making any conspicuous movements. The "short killdeer flight" was lower (3–6 m above the ground) and shorter (less than 30 sec) than the "killdeer flight," and only one bird was involved. Most often the bird flew in a straight line from one end of its territory to the other using slow, deep wing beats (which conspicuously displayed the white underwing), while "killdeer calling" repetitively.

Each unit was tabulated, timed with a stopwatch and related to both the stage of nesting and the sex of the participating individuals (if known). Individuals were sexed by their position in copulation (Bunni 1959, Phillips 1972). Known males and females were observed on alternate days. Table 1 gives the observation time for each sex at all stages of reproduction.

Eleven adults (five pairs) and 16 chicks were captured at the nest using traps modified from those designed by Coulter (1958) and by Martin (1969). All birds were banded with Fish and Wildlife Service bands and colored leg bands and uniquely dyed on various part of the plumage. Most observations prior to egg-laying were made on unmarked birds, but two Killdeers were positively identified by unusual plumage characteristics.

RESULTS

Wintering Killdeer and Early Arrivals

A few Killdeers wintered in Cache Valley. These birds tolerated close approaches (less than 3 m) by feeding conspecifics; few chases and no attacks were seen until the arrival of the migrants in early March. The migrants' presence appeared to stimulate aggression at the feeding areas. Vocalizing increased noticeably, "flight chases" occurred more frequently and feeding birds remained 30 m or more from conspecifics.

When a feeding Killdeer approached a conspecific too closely a series of "killdeer calls" was given; the "killdeer display" occurred three times under these circumstances and 22 times following territorial intrusions. In 10 of 25 observations the intruder failed to depart. In five of these 10 instances a "flight chase" ensued.

TABLE 2

NUMBER OF OCCURRENCES OF DISCRETE BEHAVIORS PER 100 H FOR MALE AND FEMALE KILLDEERS OVER ALL STAGES OF REPRODUCTION

Behavior	Males	Females	χ^{2a}
"Killdeer flight"	11.44	2.71	6.19*
"Ground chase"	51.81	37.05	3.00
Attack	53.82	1.81	54.77*
Scrape	39.02	15.36	11.96*
Initiate scrape	22.88	5.42	12.38*
Scrape exchange	14.13	46.99	22.26*
"Short killdeer flight"	26.24	9.04	10.15*
"Killdeer display"	16.15	3.61	9.01*
"Flight chase"	67.28	28.01	19.45*
"Stand off/parallel run"	12.18	6.33	2.24
"*Deet* call"	17.49	9.94	2.52

[a] All comparisons are made with df = 1.
* Indicates a significant difference between number of occurrences for males and females at the $P < 0.05$ level.

Prenesting Period

Territory establishment and agonistic behavior.—As snow melted from pastures and open fields, male Killdeers dispersed to these areas and began to set up territories. Lone males advertised by standing in elevated sites and vocalizing (Phillips 1972:1). Advertising was interrupted by 10–20 min feeding bouts. Almost all feeding was done on the territory.

Aerial intrusion by a conspecific elicited various responses by the resident male: most commonly an increased rate of calling, but also "killdeer flights" (Phillips 1972:1, 2–3). Both males and females made "killdeer flights," although males did so significantly more often (Table 2). In nine of 11 flights in which the sexes were known both participants were male. "Killdeer flights" were most frequent during prenesting (Fig. 1a).

Persistent approaches by conspecific intruders on foot resulted in "ground chases" (Phillips 1972:3–4; Fig. 2a, b, d). "Ground chases" were frequent during prenesting (Fig. 2a) and were performed nearly equally by males and females (Table 2).

When birds were more evenly matched, a "stand off/parallel run" followed the resident's approach. "Parallel running" was punctuated by "stand offs" which lasted up to 8 min (Phillips 1972:4–5). Typical sequences involved from 2–10 "parallel runs" and as many "stand offs." Any bird could attack another during a "stand off/parallel run" sequence. Females were much less likely to attack than males (Table 2; Fig. 2b), and the frequency of female-initiated attacks and "ground chases" decreased markedly as egg-laying approached.

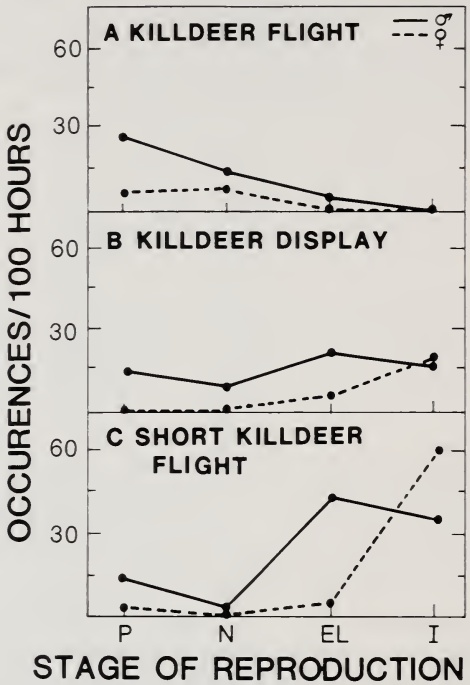


FIG. 1. Comparison of the rate of occurrence of three discrete behaviors for male and female Killdeers at four stages of the reproductive cycle. PN = prenesting period; EL = egg-laying period; I = incubation period; B = brooding period.

Females residing on established territories reacted to intruders in different ways than males. They employed less overtly aggressive displays. In response to an intruder the female resident usually moved to a nearby elevated area of the territory and "*deet* called" for 30 sec–2 min. If the intruder remained, the female approached in run/stop fashion, "*deet* calling" and sometimes "killdeer calling." As she neared the intruder, stops were more frequent and included pecking and tossing as well as short (1–4 min) bouts of preening. No female alone on the territory ever chased or attacked an intruder. The female resident preened at closest approach to the intruder.

The return of the male resident preceded "killdeer flights," "ground chasing," "stand off/parallel runs" or even attacks involving the resident male and the intruder. The returning male was apparently attracted to the site of the intrusion by the calls of the female. Resident females joined in "killdeer flights" and "stand off/parallel runs" only in the presence of their mates. Such participation declined markedly as egg laying approached.

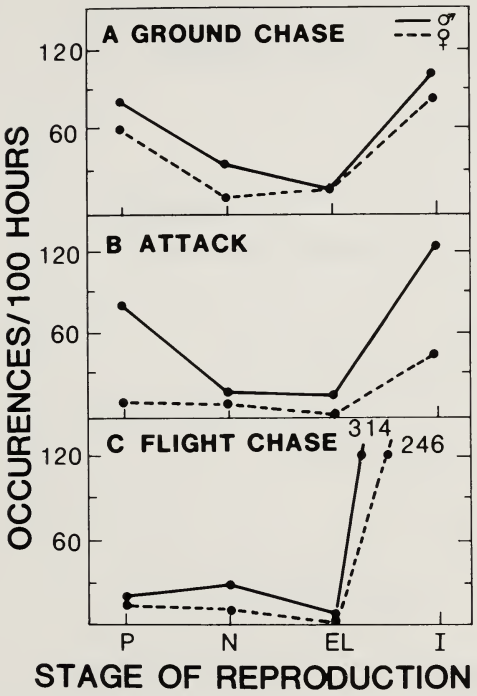


FIG. 2. Comparisons of the rate of occurrence of three discrete behaviors at four stages of the reproductive cycle. Abbreviations as in Fig. 1.

Territorial males advertised to females by scraping (Phillips 1972:1–2; Fig. 1c). Lone territorial males scraped in bouts lasting 2–20 min. Scraping is performed almost exclusively during prenesting and egg-laying and more frequently during the former (Fig. 3c). Males spent more time scraping than females ($t = 12.11$, df = 61, $P < 0.05$), except during egg-laying, and scraped significantly more often (Table 2, Fig. 3c).

Unpaired females are attracted to a scraping male and enter the potential nest-site in a complex ritualized display called the "scrape exchange" (Phillips 1972:5). Males initiated scraping in most instances; the female entered after the display had begun (Table 2, Fig. 3a, b).

Males limited their activity to their own territories. Females roamed over the territories of two or more males before pair formation. Males continued to scrape and vocalize even after they had paired, often attracting unmated females. These birds were driven off by the resident female. In seven of 22 total "ground chases" made by females, the chased bird was also a female, in another seven of these "ground chases" the chased bird was presumed to be a female because the resident male scraped or

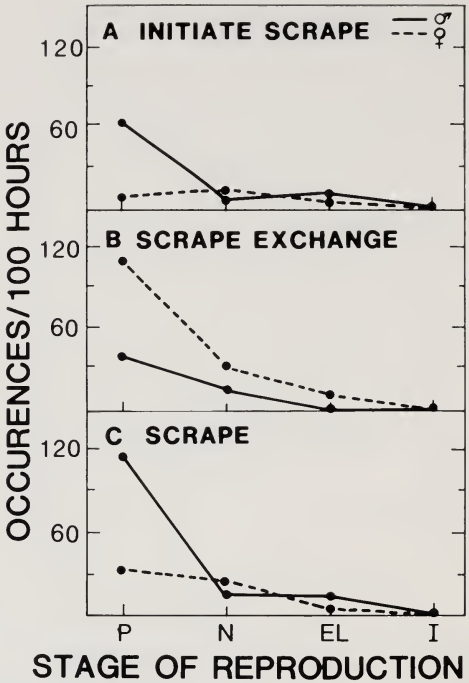


FIG. 3. Comparisons of the rate of occurrence of three discrete behaviors at four stages of the reproductive cycle. Abbreviations as in Fig. 1.

directed precopulatory approaches toward it; in the remaining eight of 22 female "ground chases" the chased bird was of unknown sex. In some of these chases the resident male also chased. In two of two attacks made by females the recipient was presumed to be a female because the resident male directed precopulatory approaches at it (the recipient).

Three mated birds copulated with birds other than their mates (Mundahl 1977). In all cases the intruding females approached the resident males when the resident female was distant; all occurred during prenesting.

Egg-laying Period

This period began when the first egg was found, or by backdating to the first egg (Bunni 1959) and ended when the complete clutch was laid.

Territory defense and agonistic behavior.—Aggressive displays used in defense of the territory were the same as those used during prenesting but their rates diminished to less than 50% of the values during prenesting (Figs. 1a, 2a, b) for both sexes combined. These decreases were significant for "ground chases" ($\chi^2 = 10.09$, df = 1, $P < 0.05$) and attacks ($\chi^2 = 11.87$, df = 1, $P < 0.05$).

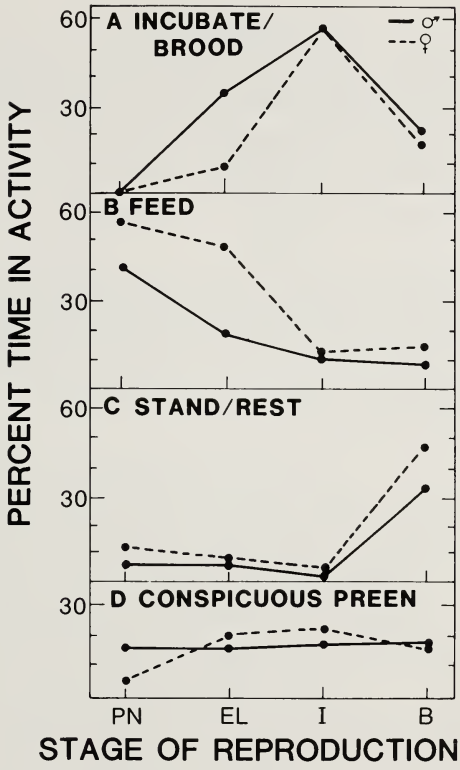


FIG. 4. Percent of time spent in four continuous behaviors by male and female Killdeers as a function of the stage of reproduction. Abbreviations as in Fig. 1. Percent values were obtained by determining the total amount of time spent by each sex in a behavior during a given stage of reproduction, dividing by the total observation time for that sex in that stage and multiplying by 100.

Nest building.—Both sexes spent significantly less time scraping during egg-laying than during the prenesting period (males: $t = 1.97$, df = 28, $P < 0.05$; females: $t = 2.90$, df = 31, $P < 0.05$).

Incubation.—Males spent more than three times as much time incubating as females during egg-laying (Fig. 4a).

Feeding.—Females spent more than twice as much time feeding as males during egg-laying (Fig. 4b) and overall (Table 3).

Incubation Period

Territory defense and agonistic behavior.—Phillips (1972) found aggression levels high during incubation, but in this study overt aggressive displays were markedly lower during incubation than at other times (Figs. 2a, b, c). "Ground chases" ($\chi^2 = 26.29$, df = 1, $P < 0.05$) and attacks

TABLE 3

COMPARISON OF MEAN DAILY PERCENT OF TIME INVESTED BY MALE AND FEMALE KILLDEERS IN CONTINUOUS BEHAVIORS OVER ALL STAGES OF REPRODUCTION[a]

Behavior	Comparison bias[b]	df	*t*
Feed	Female	125	2.280*
Distraction	Male	127	2.525*
Stand/rest	Female	124	0.564
Conspicuous preen	Male	126	0.695

[a] Daily proportion values were transformed using the inverse standard normal cumulative distribution as described by Romesburg (1976). Paired, two-tailed *t*-tests were performed using the transformed variates. This method and the arcsin transform method described by Sokal and Rohlf (1969) agreed with respect to both showing significance or non-significance 90% of the time.

[b] Sex which spent the greatest mean daily proportion of time in the behavior indicated.

* Indicates a significance difference at the $P < 0.05$ level.

($\chi^2 = 27.67$, df = 1, $P < 0.05$) declined significantly compared to prenesting values. The mean daily percent of time spent "stand off/parallel running" shows a significant decline from egg-laying to incubation (males: $t = 6.49$, df = 62, $P < 0.05$; females: $t = 3.31$, df = 59, $P < 0.05$).

During inattentive periods birds foraged and preened off the territory. Intrusion by a conspecific in a remote area of the territory elicited an approach by the resident, usually followed by a bout of preening; the intruder almost always retreated. The "killdeer display" (Fig. 1b) and "short killdeer flight" (Fig. 1c) increased in rate for both sexes during incubation. These displays were shorter and seemed less overtly aggressive than the "ground chases," attacks and "killdeer flights" employed earlier.

Incubation and nest defense.—The sexes shared incubation nearly equally during the daylight hours (Fig. 4a). However, males seemed to perform most nocturnal incubation. I trapped one bird from each of four marked pairs on the nest on five different nights at 21:30, 22:00, 01:00, 01:00, and 05:30; all were male. In addition, I observed three marked pairs (10 days–3 weeks into incubation) on six consecutive evenings. The male initiated incubation before dusk and no incubation exchanges were made by nightfall. Time spent at the nest increased during incubation for both sexes (Fig. 4a). Females were more reluctant to approach a disturbed nest. Trapping success at the nest was 89% for males and 35% for females.

The presence of a predator elicited rapid "*deet* calling" from the inattentive bird. One or both birds began to distract the predator. Distraction behavior occurred during prenesting but increased significantly for males after the eggs were laid ($t = 2.69$, df = 64, $P < 0.05$). Males spent significantly more time distracting than females (Table 3).

Brooding Period

Agonistic activities.—The most conspicuous features of the brooding period were the cessation of the boundary defense of the nesting territory and the increased intraspecific aggression, especially by females. As soon as the clutch hatched, resident Killdeers ceased defending areas of their nesting territory and only defended an area around their brood varying in radius from 20–40m.

Behavior was similar to that employed in territorial establishment during prenesting. Pronounced increases in the rates of "ground chases" (Fig. 2) are statistically significant for both sexes (males: $\chi^2 = 17.50$, df = 1, $P < 0.05$; females: $\chi^2 = 9.71$, df = 1, $P < 0.05$) and increases in attacks were statistically significant for males ($\chi^2 = 64.02$, df = 1, $P < 0.05$; females: $\chi^2 = 2.73$, df = 1, $P < 0.05$). Females were considerably more aggressive during brooding than previously.

The "flight chase" was the most frequent method of repelling conspecifics during brooding (Fig. 2c). The difference in the rate of flight chasing between incubation and brooding was statistically significant for both sexes (males: $\chi^2 = 155.73$, df = 1, $P < 0.05$; females: $\chi^2 = 43.74$, df = 1, $P < 0.05$). Figure 1c shows the increase in "short killdeer flights" during brooding for females: this display advertised the presence of the pair and was less time consuming than the "killdeer flight."

Brooding.—Attentive birds were very conspicuous during brooding. They kept contact with the brood by remaining stationary and "*deet* calling" continously during early mornings and late evenings though less in midday. Males and females spent similar proportions of time "*deet* calling" during brooding ($t = 0.11$, df = 16, $P < 0.05$). Males spent about the same amount of time brooding as females (Fig. 4a; excluding one of three successful pairs in which the females deserted).

Female desertion.—The only marked female to hatch a second clutch deserted immediately after hatching, but two marked females that produced successful first clutches were attending their broods 12 days after hatching when I terminated my observations.

DISCUSSION

Trivers (1972) defined parental investment as "any investment by the parent in an individual offspring which increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring." Trivers (1972) believed that in monogamous bird species, females invest slightly more in a single clutch than males. To rigorously test Trivers' (1972) hypothesis would require information on energy expenditures as well as the effects of given behavior

patterns on future reproductive success. Such information is difficult to obtain in a field study. However, quantitative data on parental care can be obtained (Burger 1981, Pierotti 1981) and certainly represent a type of parental investment which will affect the ecological success and mating strategies of the sexes within a given species.

My data on parental care indicate that the degree of role specialization practiced by Killdeers tends to equalize the parental investment by each sex over a given breeding season. For brevity and convenience I follow Trivers (1972) in employing the language of reproductive strategy in explaining what adaptations natural selection would be expected to favor.

In Killdeers both sexes incubate, brood, and show similar agonistic behaviors. The degree to which role specialization occurs appears to be dictated by the reproductive energy demands for each of the sexes. As noted by King (1973) and Ricklefs (1974) female birds produce gametes with a large amount of stored energy, whereas the male's energy expenditure in gamete production is minimal. Since female Killdeers lay eggs in rapid sequence (nearly an egg per day, on the average) (Furniss 1933, Bunni 1959), and frequently replace clutches (Bunni 1959), their energy demand for oogenesis must be considerable. Accordingly, the females' behavior prior to incubation should tend to minimize energy expenditures not related to gamete production while increasing those activities which contribute to successful production of eggs.

Since food deprivation produces a more severe depression of reproductive output in female birds than in males (Assenmacher et al. 1965, King 1973, Ricklefs 1974), it would seem advantageous that male Killdeers assume the metabolically more costly tasks of nest-building, territory defense, and incubation during prenesting and egg-laying while females are mobilizing energy for egg production or recuperation from egg production.

Prenesting and Egg-laying Periods

Agonistic and territorial behavior.—In this study the female Killdeer's role in territorial establishment was shown to be minimal. Males performed "killdeer flights," "short killdeer flights," and scraping displays significantly more often than females (Table 2). These displays are conspicuous visually and acoustically and probably serve to communicate the performer's presence as a form of territorial advertisement.

The female Killdeer's role in territorial defense was one of secondary importance. Males made significantly more "killdeer displays," "flight chases," and attacks than females (Table 2; Figs. 1b; 2b, c); these displays are aggressive. Attacks may expose the attacker to retaliation or involvement in prolonged fighting representing a potentially large energy investment or increased risk of predation during fighting. Jaeger (1981) conclud-

ed that attacks between red-backed salamanders (*Plethodon cinereus*) could inflict injuries which would impair the opponent's biological fitness. During prenesting and egg-laying, females chased intruders of unknown sex only when their mates also chased.

Paired female Killdeers seemed to restrict overt aggressive activities to encounters with other females during early prenesting; they also performed more passive displays which could discourage intrusion of the territory by other females. Females and males employed the "stand/rest" and "preen" about equally during the discrete stages of reproduction (Fig. 4c, d) as well as throughout the reproductive cycle (Table 3). Although these are not overtly aggressive displays, Geist (1974) concluded that in a monomorphic species the presence of an individual of either sex discourages trespass of territory.

The increase in the proportion of time spent feeding (Fig. 4b) and the decrease in the occurrence of aggressive actions by female Killdeers near the end of prenesting suggest that they were mobilizing maximum energy for egg production at that time.

Male reproductive strategy and mate defense by females.—Phillips (1972) noted a case of a male Killdeer directing precopulatory behavior toward a strange female near his nest and suggested that males could respond to females even late in incubation. In this study, males directed precopulatory displays toward any female that was present. If the male's mate returned while another female was present, he then assisted the resident female in chasing the intruder away.

As noted by Trivers (1972), the optimal breeding strategies of the two sexes are rarely identical. The male maximizes his fitness by inseminating as many females as possible. However, the male can also increase his fitness by caring for his eggs and young and by defending his territory, and can be expected to exhibit a high degree of territorial and parental behavior. A more extreme example of this two-pronged male strategy occurs in the Mountain Plover (*Charadrius montanus*) in which at least some males mate with one female and assume all incubation duties for that female's clutch but remain sexually active (Graul 1974). In species in which male parental investment is large, the female maximizes her fitness by defending her mate from potential competitors (Orians 1969). Tinbergen (1939) stressed the importance of female-female aggression in the Snow Bunting (*Plectrophenax nivalis*) in maintaining monogamy in that species. Morton et al. (1978) quantified aggressive responses of female Eastern Bluebirds (*Sialia sialis*) to models of female conspecifics and postulated that the high levels of aggression serve to ensure a paired female of maximum continued investment from her mate after she has laid. Graul (1974) noted that in the Mountain Plover males tend to react aggressively toward

males and females behave aggressively toward females. In the Killdeer, female-female aggression probably serves to stabilize the pair bond.

An inseminated female whose mate has deserted her and remated faces a larger energy investment if she must care for the clutch/brood unaided. In the long run, the female may conserve energy by defending her mate from competitors, thus ensuring that he will contribute to the rearing of the young.

The most common forms of aggressive behavior witnessed in female-female encounters were the "ground chase" and the "flight chase." Figure 2a, c show that the frequency of occurrence of "ground chases" and "flight chases" by females closely parallel the frequency of occurrence of the same behaviors by males at each stage of the reproductive cycle. These displays convey a high likelihood of attack and should be efficient for repelling intruding females. Except for brooding, the rates of occurrence of these behaviors are highest during prenesting and during prenesting these displays are most often directed at other females. Mate defense is probably most critical during prenesting when many potential competitors are yet unmated.

The advantages of extra-pair copulation by mated females of monogamous bird species were reviewed by Gladstone (1979). In this study one of three females involved in non-monogamous copulation appeared to be already paired with a male; the other two females could not be positively identified.

Incubation Period

Incubation and brood defense.—Norton (1973) estimated the heat requirement in the Dunlin (*Calidris alpina*) at 120% of BMR using Kendeigh's (1963) equation. Ricklefs (1974) and Kendeigh (1973) contended that the energy requirement for incubation must be supplied largely by supplemental heat production, especially in open-nesting species, but King (1973) believed that incubation entailed no additional cost. I have presented evidence that the male Killdeer performs most (or all) of the night incubation. At night the energy cost would be higher than during the day, especially early in the breeding season. Night incubation by the male leaves the female free to feed, seek shelter, and reduce energy expenditure during this time. The incubating bird may also increase its investment by rendering itself more susceptible to predation by incubating at night (Burger 1974; T. A. Sordahl, pers. comm.).

Distraction behavior is believed to enhance the survival of the eggs or young by directing a potential predator's attention toward the parent bird. A bird may render itself more vulnerable to predation or injury by displaying closer to or even attacking the predator (Smith 1969, Myers 1978,

Denson 1979). Table 3 shows that males spent significantly more time giving distraction displays than females on a mean time per day basis. The male's investment in clutch and brood defense is thus greater than that of the female. Likewise, the female Killdeer's hesitation to approach a disturbed nest may render her less susceptible to predation at the nest than the male.

Brooding Period

Agonistic behavior and brood defense.—Females and males markedly increased their rates of display and aggressive activities during the brooding period (Figs. 1b; 2a, b, c). The increase in display and agonistic activity by the female seems paradoxical unless viewed as a means by which the fitness of the parent is maximized. Once a clutch has hatched, aggressive brood defense is probably selected for, rather than conservation of energy for possible replacement of clutches. Mace (1971) presented data which suggest that fledging success is higher than hatching success in Killdeers. Defense of the brood during this period may provide high returns in reproductive success. There is also less time to produce another brood.

Görannsson et al. (1975) demonstrated that the aggressive behavior of Northern Lapwings (*Vanellus vanellus*) decreased the predation rate on artificial lapwing nests placed in lapwing territories relative to those placed outside their breeding territories. Kruuk (1964) believed that attacks by Common Black-headed Gulls (*Larus ridibundus*) on potential predators improved the chances for successful hatching of the gulls' young. The increase in aggression of female Killdeers during brooding probably increases the chances of chick survival.

Desertion by females.—Several workers have noted that it is common for female Killdeers to desert the brood shortly after hatching (Bunni 1959; R. E. Phillips, pers. comm.; Mundahl, pers. obs.), especially late in the breeding season. This phenomenon has been reported for other monogamous shorebirds (Lenington 1980). The potential adaptive advantages of Killdeer female desertion are treated by Lenington (1980), who suggested that female Killdeers deserted when physiologically taxed by the stress of egg production. Perrone and Zaret (1979) also suggested that differences in the ability of the parents to provide parental care may dictate which sex is most likely to desert.

SUMMARY

The behavior patterns of the Killdeer (*Charadrius vociferus*) during the nesting cycle are reviewed. The frequencies of occurrence of discrete behaviors were monitored for each sex during the prenesting, egg-laying, incubation, and brooding periods and are compared graphically. Continuous behavior patterns were timed, and the total and average amounts of time

spent performing these behavior patterns were compared for male and female Killdeers during these four stages of the breeding cycle.

The roles of breeding male and female Killdeers are discussed with emphasis on the energetic demands and reproductive strategies of each sex. I propose that male Killdeers tend to compensate for the large energy investment of the female by taking a greater part in territorial establishment and defense, parental behavior, and nest and brood defense. The male assumed the major role in territorial establishment and defense during the prenesting and egg-laying period. The female defended her mate from other females through egg-laying but her role in territory defense was limited to passive displays, whereas the male manifested intolerance of intruders by active displays, chasing, and attacks. The male also assumed the major role in nest building and incubation. The greater proportion of time spent distracting by males and probable higher proportion of night incubation by males may represent higher parental investment due to increased risk of predation.

ACKNOWLEDGMENTS

It is a pleasure to thank Keith L. Dixon for his advice and encouragement throughout the course of this study. S. B. Vander Wall, W. D. Graul, T. A. Sordahl and R. E. Phillips read drafts of this manuscript and their critical comments are appreciated. H. Charles Romesburg and D. V. Sisson advised me in statistical matters. I appreciate the encouragement and support of Amy Eisenberg throughout the study. This study was supported in part by a Utah State University Research Fellowship.

LITERATURE CITED

Assenmacher, I., A. Tixier-Vidal, and H. Astier. 1965. Effets de la sous alimentation de jeûne sur la gonado stimulation du canard. Ann. Endocrin. 26:1–26.

Bunni, M. K. 1959. The Killdeer, *Charadrius v. vociferus* Linneaus, in the breeding season: ecology, behavior and the development of homiothermism. Ph.D. diss., Univ. Michigan, Ann Arbor, Michigan.

Burger, J. 1974. Breeding adaptations of Franklin's Gull (*Larus pipixcan*) to a marsh habitat. Anim. Behav. 22:521–567.

———. 1981. Sexual differences in parental activities of breeding Black Skimmers. Am. Nat. 117:975–984.

Bursian, S. J. 1971. The structure and function of Killdeer vocalizations. M.S. thesis, Univ. Minnesota, St. Paul, Minnesota.

Coulter, M. W. 1958. A new waterfront nest trap. Bird-Banding 29:236–241.

Denson, R. D. 1979. Owl predation on a mobbing crow. Wilson Bull. 91:133.

Emlen, S. T. and L. W. Oring. 1977. Ecology, sexual selection and the evolution of mating systems. Science 197:215–223.

Furniss, O. C. 1933. Observations on the nesting of the Killdeer Plover in the Prince Albert district in central Saskatchewan. Can. Field-Nat. 47:135–138.

Gladstone, D. E. 1979. Promiscuity in monogamous colonial birds. Am. Nat. 114:545–557.

Giest, V. 1974. On the relationship of social evolution and ecology in ungulates. Am. Zool. 14:205–220.

Görannsson, G., J. Karlson, S. G. Nilsson, and S. Ulfstrand. 1975. Predation on birds' nests in relation to antipredator aggression and nest density: an experimental study. Oikos 26:117–120.

Graul, W. D. 1974. Adaptive aspects of the Mountain Plover social system. Living Bird 12:69–94.

———, S. R. Derrikson, and D. W. Mock. 1977. The evolution of avian polyandry. Am. Nat. 111:812–816.

Hildén, O. 1975. Breeding system of Temminck's Stint (*Calidris temminckii*). Ornis Fenn. 52:117–144.

Jaeger, R. G. 1981. Dear enemy recognition and the costs of aggression between salamanders. Am. Nat. 117:962–974.

Jenni, D. A. 1974. Evolution of polyandry in birds. Am. Zool. 14:129–144.

——— and B. J. Betts. 1978. Sex differences in nest construction, incubation, and parental behavior in the polyandrous American Jacana (*Jacana spinosa*). Anim. Behav. 26:207–218.

Kendeigh, S. C. 1963. Thermodynamics of incubation in the House Wren (*Troglodytes aedon*). Proc. XIIIth Int. Ornithol. Congr., 884–904.

———. 1973. Discussion. Pp. 311–320 *in* Breeding biology of birds (D. S. Farner, ed.). Nat. Acad. of Sci., Washington, D.C.

King, J. R. 1973. Energetics of reproduction in birds. Pp. 78–107 *in* Breeding biology of birds (D. S. Farner, ed.). Nat. Acad. of Sci., Washington, D.C.

Kruuk, H. 1964. Predators and anti-predator behavior of the Black-headed Gull (*Larus ridibundus* L.). Behaviour Suppl. XI.

Lenington, S. 1980. Biparental care in Killdeer: an adaptive hypothesis. Wilson Bull. 92: 8–20.

Mace, T. 1971. Nest dispersion and productivity in Killdeers (*Charadrius vociferus*). M.S. thesis, Univ. Minnesota, St. Paul, Minnesota.

Martin, S. G. 1969. A technique for capturing nesting grassland birds with mist nets. Bird-Banding 40:233–237.

Morton, E. S., M. S. Geitgy, and S. McGrath. 1978. On bluebird "responses" to apparent female adultery. Am. Nat. 112:968–971.

Mundahl, J. T. 1977. Role specialization in the parental and territorial behavior of the Killdeer. M.S. thesis, Utah State Univ., Logan, Utah.

Myers, J. P. 1978. One deleterious effect of mobbing in the Southern Lapwing (*Vanellus chilensis*). Auk 95:419.

Norton, D. W. 1973. Ecological energetics of calidridine sandpipers breeding in northern Alaska. Ph.D. diss., Univ. Alaska, Fairbanks, Alaska.

Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. Am. Nat. 103:589–603.

Oring, L. W. and M. L. Knudson. 1972. Monogamy and polyandry in the Spotted Sandpiper. Living Bird 11:59–73.

——— and S. J. Maxson. 1978. Instances of simultaneous polyandry by a Spotted Sandpiper (*Actitis macularia*). Ibis 120:349–353.

Parmelee, D. F. and R. B. Payne. 1973. On multiple broods and the breeding strategy of arctic Sanderlings. Ibis 115:218–226.

Perrone, M., Jr., and T. M. Zaret. 1979. Parental care patterns in fishes. Am. Nat. 113:351–361.

Phillips, R. E. 1972. Sexual and agonistic behavior in the Killdeer (*Charadrius vociferus*). Anim. Behav. 20:1–9.

Pierotti, R. 1981. Male and female parental roles in the Western Gull under different environmental conditions. Auk 98:532–549.

Pitelka, F. A., R. T. Holmes, and S. A. MacLean. 1974. Ecology and evolution of social organization in arctic Sandpipiers. Am. Zool. 14:185–204.

Ricklefs, R. E. 1974. Energetics of reproduction in birds. Pp. 152–297 *in* Avian energetics (R. A. Paynter, ed.). Publ. Nuttall Ornithol. Club, No. 15.

ROMESBURG, H. C. 1976. Use of the normal generated distribution for estimating population survival. J. Theoret. Biol. 61:447–457.

SOKAL, R. R. AND R. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, California.

SMITH, N. G. 1969. Provoked release of mobbing—a hunting technique of *Micrastur* falcons. Ibis 111:241–243.

TINBERGEN, N. 1939. Field observations of east Greenland birds. II. The behaviours of the Snow Bunting in spring. Trans. Linn. N.Y. 5:1 -94.

TRIVERS, R. L. 1972. Parental investment and sexual selection. Pp. 136–179 *in* Sexual selection and the descent of man 1871–1971 (B. Campbell, ed). Aldine Publishing Co., Chicago, Illinois.

DEPT. BIOLOGY AND THE ECOLOGY CENTER, UTAH STATE UNIV., LOGAN UTAH 84322. (PRESENT ADDRESS: ELM VALLEY VETERINARY CLINIC, P.O. BOX 295, ELMWOOD, WISCONSIN 54740.) ACCEPTED 15 NOV. 1981.

FRANK M. CHAPMAN FUND—DEADLINE CHANGE

The Frank M. Chapman Memorial Fund gives grants in aid of ornithological research and also post-doctoral fellowships. While there is no restriction on who may apply, the Committee particularly welcomes and favors applications from graduate students; projects in game management and the medical sciences are seldom funded. **Applications for projects in 1983 should be submitted not later than 15 February; prospective applicants and advisors should note there will shortly be a change in the Chapman meeting and deadline schedule.** Application forms may be obtained from the Frank M. Chapman Memorial Fund Committee, The American Museum of Natural History, Central Park West at 79th St., New York, New York 10024.

NEW PUBLICATION

Cornell University's Laboratory of Ornithology announces the publication of a new magazine devoted to the study of birds, The Living Bird Quarterly. For further information write Laboratory of Ornithology, Sapsucker Woods, Ithaca, New York 14850 ([607] 256-5056).

Wilson Bull., 94(4), 1982, pp. 531–545

BIOLOGY AND BEHAVIOR OF BREEDING PIPING PLOVERS

Winifred E. Cairns

The Piping Plover (*Charadrius melodus*) is an endemic species of central and eastern North America which breeds discontinuously throughout its range in suitable sand beach habitat. Apart from early accounts such as those by Bent (1929) and Wilcox (1939), a single study by Wilcox (1959) provides most of the breeding information known for the species. An assessment of the numerical status of the population in eastern North America is contained in Cairns and McLaren (1980). The present study was undertaken to obtain baseline information on the Piping Plover in Nova Scotia. Emphasis was placed on detailing the biology and behavior associated with the nesting cycle, and on examining the relationship between nesting success and the multiple use of beaches.

STUDY AREA AND METHODS

The major study area was at Cadden Beach, southern Nova Scotia (43°50′N, 64°50′W), and consisted of a sandspit 1.4 km long and 75–200 m wide. This broad, relatively flat expanse of unconsolidated sand was strewn with gravel, clods of peat, driftwood, and other debris. Across most of the spit vegetation was extremely scanty, consisting of seabeach sandwort (*Arenaria peploides*) and to a lesser extent marram grass (*Ammophila breviligulata*). Studies at this site were carried on from 1 May–15 August 1975 and from 22 April–10 August 1976. Additional data were obtained from May–August 1976 during visits to eight other beaches in Nova Scotia where *C. melodus* breeds, and from observations in 1977, 1978, and 1979 at numerous breeding sites throughout Atlantic Canada.

Adult Piping Plovers were captured on their nests by a drop trap or a circular walk-in trap. Adults were sexed by a combination of behavior and plumage characteristics: in general the male of a pair had the darker neck band. Chicks were banded as they hatched or when first encountered. I banded 14 adults and 53 chicks in 1975, and 11 adults and 91 chicks in 1976. Nineteen adults in 1975 and four in 1976 were color marked. After hatching, chicks were recaptured and weighed as often as possible.

In 1976 I estimated 27–29 pairs of Piping Plovers were present and 96 chicks were hatched on Cadden Beach (based on the number of chicks encountered from known nests compared with numbers encountered from nests not found by me, as well as other circumstantial evidence). Approximately 10 non-breeding birds also occupied the beach each year.

RESULTS AND DISCUSSION

Fidelity to nesting area.—In Nova Scotia most Piping Plovers arrive from mid- to late April and initially feed in areas unclaimed as territories, where aggressive interactions are numerous. Such early-season flocking places birds of both sexes in close proximity, and in high density beaches may speed up the development of behavior associated with territorial es-

tablishment and courtship. This is suggested by later hatching dates for beaches where only one or two pairs occur.

At least some birds returned to their territories a second year. Two females caught on Cadden Beach nests in 1976 had occupied the same territories in 1975. Both nested within 20 m of their nest-sites of the previous year. A male occupied a 1976 nesting territory that was about 1 km from his 1975 birthplace. Five other adults already banded when observed on Cadden Beach in 1976 had probably been banded there in 1975 by me.

The tendency for adults to return to a former breeding area (and sometimes nesting territory as well) has been reported for Piping Plovers (Wilcox 1959) as well as for a number of other plover species including Ringed Plover (*C. hiaticula*) (Laven 1940, Bub 1962), Killdeer (*C. vociferus*) (Lenington and Mace 1975), Kentish Plover (*C. a. alexandrinus*) (Rittinghaus 1956), Mountain Plover (*C. montanus*) (Graul 1973b) and Northern Lapwing (*Vanellus vanellus*) (Spencer 1953). Few first year birds return to breed in the area of hatching among *Charadrius* plovers, as suggested by ca. 5% return rates for Ringed, Piping and Kentish plovers (Lenington and Mace 1975).

Spacing and territory size.—Of the approximately 0.2 km^2 of raised sandspit on Cadden Beach, about 0.12 km^2 was prime Piping Plover nesting habitat, and was largely divided up into about 28 contiguous nesting territories, ranging from 500–8000 m^2 and averaging about 4000 m^2 in size. Feeding territories on the tidal sandflats were defended seaward from stretches of shoreline 50–100 m long. Nesting and feeding territories were usually contiguous, except in densely populated areas where some birds had to cross neighboring nesting territories to reach their feeding territories. Both types of territories were maintained throughout the season by breeding pairs. Unmated males, non-breeding pairs, and pairs that lost a clutch or brood too late to renest also maintained both kinds of territories. Distances to nearest neighboring nests on Cadden Beach averaged 51 m for the 23 nests found in 1975 and 53 m for the 27 nests in 1976 (including three known renests). The closest simultaneously active nests were 3 m apart.

Territory sizes among plovers vary greatly ranging from 190 m in Wilson's Plover (*C. wilsonia*) (Tomkins 1944) to 0.16 km^2 in Mountain Plover (Graul 1973b). Size of territory probably reflects, at least in part, the relative amounts of feeding done within the territory and in areas outside. The Red-capped Dotterel (*C. ruficapillus*) population described by Hobbs (1972) fed at a site 3 km from the breeding grounds, probably an extreme case of distance between feeding and nesting sites. Ringed Plovers (Mason 1947) and Little Ringed Plovers (*C. dubius*) (Simmons 1956) have been reported to feed mainly on neutral feeding areas, while Mountain (Graul

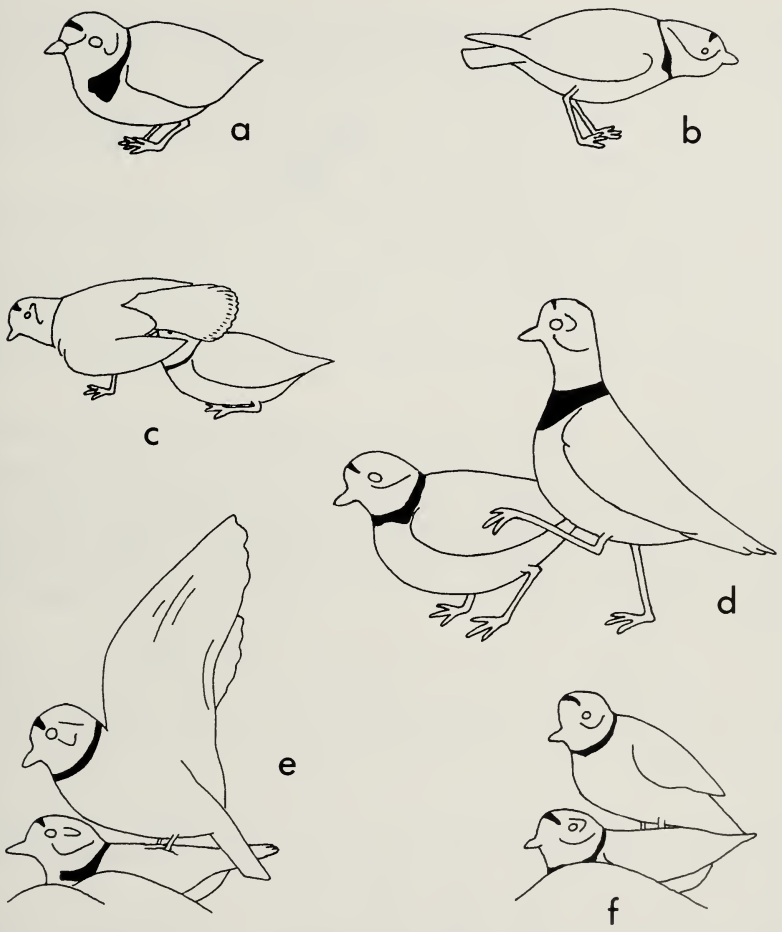


FIG. 1. Courtship postures: (a) territorial male with exaggerated neck band, (b) posture used during low gliding run, (c) female thrusting beak among feathers beneath male's tail, (d) male performing rapid high-stepping tattoo beside female, (e) mounting, and (f) copulation.

1973b) and Piping plovers do most of their feeding within their own territories.

TERRITORIAL BEHAVIOR

Establishment and maintenance.—Upon arrival males begin to establish territories; 8–10 had been set up when observations began on 22 April 1976. During territorial establishment, males spend much time on their prospective nesting territories. Thoroughly traversing the area in brief

flights and runs, they stop periodically and remain motionless except when scanning or preening (Fig. 1a). Scanning occurs at intervals and involves slowly rolling the upwardly tilted head from one side to the other. Most preening, which may last for 2 or 3 h at a time, is concentrated on the neck ring and makes it appear wider and darker. Long periods on the ground are interrupted by aerial displays and calls.

Intruders are met with horizontal threat charges, and ground or aerial chases, which aid in establishing rough territorial boundaries. These may undergo modification throughout the season as parallel run or horizontal threat displays maintain boundaries, or produce gains or losses in territory size. Agonistic activity towards neighboring birds is shown by both sexes although the male plays the greater role, particularly during territorial establishment.

Aerial displays.—Males perform elaborate flights above their territories apparently to advertise ownership to rival males and prospective females. In flight, deep, slow wing-beats and an alternate tilting of the body from side-to-side produce a fluttering flight, making the bird more conspicuous than in normal flight. Display flights, which last up to 30 min, traverse elliptical and figure eight courses from just above ground level up to ca. 35 m.

Aerial displays are usually accompanied by calls. The more common call is a continuous rapid series of high-pitched calls and sometimes is interspersed with a series of long drawn-out mournful-sounding calls.

Aerial displays and calls can arise unprovoked or can be elicited by females or other males. Sometimes two birds perform flying within a few meters of each other: these may be rival males on adjacent territories or, on occasion, mated pairs. Aerial displays and calls are sometimes given on moonlit nights but very rarely on dark nights.

Display flights and calls decline with the onset of egg-laying and incubation. One lone male that failed to attract a mate performed courtship displays regularly from the start of the 1975 field season until 19 July.

The aerial display flight of the Piping Plover resembles that described for Killdeer by Phillips (1972), and Ringed, Little Ringed, and Kentish plovers by Witherby et al. (1965).

Horizontal threat display.—Most horizontal threat displays take the form of a charge. In assuming this display posture the bird leans forward on slightly bent legs with head drawn well back into the body (Fig. 2). The neck ring becomes prominent and with increasing intensity the wings are slightly raised and the feathers of the breast, sides, and upper back are puffed. At greatest intensity the tail is fanned open and depressed, while the feathers of the back, sides, and upper breast are raised to give a ragged appearance. The low intensity display is given within a small flock by one

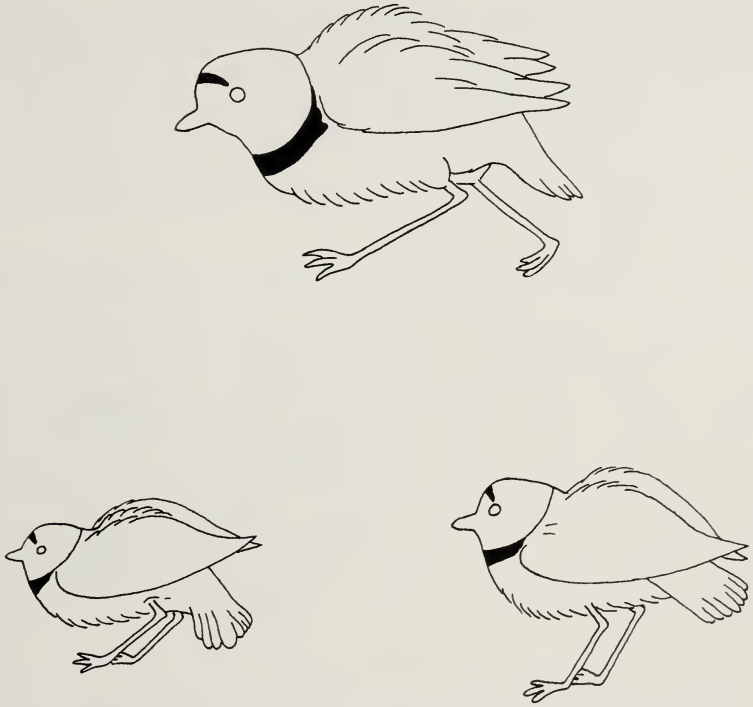


FIG. 2. Some postures used during horizontal threat display.

or more birds using low gliding runs. Then charging birds usually swerve before reaching the target bird and continuously redirect their displays toward other individuals so that actual chases and fights seldom ensue.

Encounters between two individuals more often lead to high intensity display and chases at least 30 m in length. The charging bird adopts a low intensity threat posture in a low gliding run, then increases speed and intensity. At close quarters high intensity charges occasionally terminate in brief fights. The combatants initially face each other in horizontal threat display and then jump and fly at each other, striking the bill and wings against the head, neck, and upper back regions of the opponent. Most skirmishes subsided within a few minutes as the birds gradually moved apart, often vigorously pecking the ground, or running with abrupt stops and starts. Horizontal threat displays were accompanied by a series of low rattling calls which became increasingly more rapid and took on a whirring throaty undertone as the display progressed.

Various forms of the horizontal threat display have been reported for a number of other plover species including Ringed Plover (Edwards et al.

1947, Mason 1947, Simmons 1953b), Semipalmated Plover (*C. semipalmatus*) (Sutton and Parmelee 1955), Little Ringed Plover (Simmons 1953b), Wilson's Plover (Tomkins 1944), Killdeer (Phillips 1972), Mountain Plover (Graul 1973a, 1973b) and Blacksmith Plover (*Hoplopterus armatus*) (Hall 1964). The threat display of the Piping Plover most closely resembles those of the Killdeer and Ringed Plover. These two species enlarge the neck markings and the breast feathers by fluffing them to present a rounded frontal appearance to the protagonist.

Parallel-run display.—After the establishment of territorial boundaries parallel-run displays, in which two neighbors run in parallel along a common boundary, increase in importance. Both birds adopt stiffly erect postures with heads and necks stretched upward, breast feathers puffed smoothly, and dark sides of the neck and neck ring showing sharply against the white (Fig. 3). After facing each other and head-bobbing, one bird turns at right angles and runs rapidly for a distance of 1–10 m along the disputed line. In the same manner the second bird runs past the first, often arcing into its own territory before stopping abruptly ahead of the first bird. The birds move alternately, abruptly terminating each spurt by assuming a more sharply erect posture, and bobbing the head several times.

In more intense encounters running may be interspersed with violent bouts of pecking the ground. Bouts of head-bobbing alternate with very short rapid runs, and a combination of shoulder-to-shoulder and breast-to-breast shoving may occur. Between high intensity parallel runs, close range horizontal threat charges may take place. Low intensity parallel-run displays are expressed by parallel walking or by a form of upright display in which the two opponents face each other and engage in bouts of head-bobbing alternated with neck preening or ground pecking.

The normal parallel run may cover distances of up to 100 m before the birds reverse direction and repeat the display. Encounters may continue 30 min or more, and usually conclude with the gradual withdrawal of both birds, pecking the ground as they move away from the final location of the boundary on that occasion. Vocalizations used during parallel-run displays are similar to those accompanying horizontal threat displays.

Upright threat postures have been reported in Ringed, Little Ringed and Kentish plovers (Simmons 1953b), Killdeer (Phillips 1972), Wilson's Plover (Tomkins 1944) and Mountain Plover (Graul 1973b), but only Killdeer and Mountain Plover are known to use the displays in conjunction with parallel runs. Interestingly, Ringed and Little Ringed plovers, when in upright threat display rapidly run in place, in a manner similar to the pre-mounting behavior of the Piping Plover. The general pattern among plover species of a head-up posture for defense threat and head-down posture for aggressive threat (Maclean 1972) also holds true for Piping Plovers.

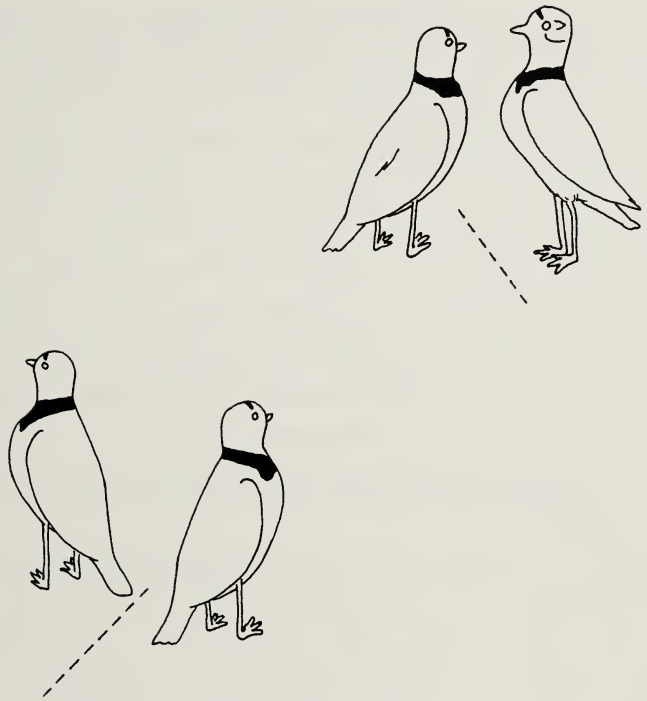


FIG. 3. Upright postures used during parallel-run displays along a common boundary.

COURTSHIP

Scraping.—A courting male on territory walks about with deliberate movements, often tossing aside sea shell fragments. Periodically he stops, squats, and, leaning far forward on his breast, pivots to the left and right, while simultaneously kicking sand backwards, producing a shallow depression or scrape in the sand. During pauses he occasionally utters one or both advertisement calls, or tosses bits of shell from the rim of the scrape into the depression beneath him. When a female is nearby the male walks or runs on bent legs, with head lowered and tail sometimes spread and elevated, squatting briefly in a number of his scrapes, of which there may be 20 or more (Fig. 1b). If the female approaches closely, the scraping male erects and spreads his tail, and increases the tempo of rotations in the scrape. Occasionally, a female following a courting male will also scrape briefly.

Tilt display.—With the female close by, the male may perform a tilt display, slowly rising to stand stiffly upright in the scrape, head, body, tail, and the partly or completely spread wings all being held in one plane, with tail elevated at an angle of about 30° (Fig. 1c). The female crouches

slightly behind the male and thrusts her beak one or more times among the feathers below the base of his tail. Alternatively, the female may approach from the side, and creeping under the male's horizontally spread tail, nestle into the sand beneath it, her body perpendicular to his. The tilt display may be repeated several times in succession at different scrapes, or the female may walk a short distance away, adopting a slightly crouched stance with legs somewhat spread, and await the approach of the male.

Mounting and copulation.—Advancing toward the female, the male slips into a low gliding crouch with head held below the horizontal and drawn well into the body. Nearing her, he gradually rises into a very erect posture with neck outstretched, neck ring conspicuously broadened and breast expanded. Simultaneously he beats a high-stepping and increasingly rapid tattoo with both feet (Fig. 1d). Upon reaching the female the male may stand by the base of her tail and continue the tattoo for a few minutes longer before flapping his wings and mounting (Fig. 1e). Copulation takes up to 1.5 min. Both birds often preen after copulation. No post-copulatory displays were seen.

Courtship in the Piping Plover basically resembles that of *Charadrius* spp. as demonstrated by Little Ringed Plover (Sluiters 1938, Simmons 1953a), Ringed Plover (Laven 1940), Snowy Plover (*C. a. nivosus*) (Boyd 1972), Mountain Plover (Graul 1973b), and Killdeer (Phillips 1972). However, none of these authors mentioned the female thrusting her bill among the feathers beneath the male's tail, as indicated above in the Piping Plover. Other differences between *C. melodus* and *Charadrius* spp. occur in the position of the wings during the tilt display; both Little Ringed (Glutz et al. 1975) and Piping plovers spread their wings on a uniform plane, while the Snowy and Mountain plovers droop the wing which is toward the female. The Killdeer apparently does not spread its wings.

The details of mounting and copulation differ somewhat with plover species. In most, males approach females in a low gliding run which somewhat resembles the posture used during low intensity horizontal threat. Before actually mounting the female, male Snowy Plovers (Boyd 1972), Red-capped Dotterels (Hobbs 1972), Killdeer (Phillips 1972), and Mountain (Graul 1973b) and Wilson's plovers (Tomkins 1944), as well as Piping Plovers adopt an upright precopulatory posture with rapid high-stepping foot movements. The Snowy (Boyd 1972) and Wilson's plovers (Tomkins 1944) are apparently the only species in which males grasp the female's neck feathers with their bills during copulation. Piping Plovers copulate anywhere within their nesting and feeding territories but Snowy Plovers (Boyd 1972), Killdeer (Phillips 1972), and Mountain Plovers (Graul 1973b) apparently only copulate at nest or scrape sites.

DISTRACTION BEHAVIOR

Piping Plovers respond to intruders (avian, human, and other mammalian) by squatting, false brooding, high-tailed running, crouch run, and injury feigning. During highest intensity distraction constant "whirring" vocalizations may be emitted. Some displaying birds have come within 2 m of me while others, after initially approaching me, have been observed to feign injury continuously while travelling up to 100 m away. Distraction display may occur at any time during the breeding season, although it is usually most frequent and intense about the time of hatching. Both birds of a pair may simultaneously engage in distraction displays, especially in areas of high density of nests or broods, when as many as a dozen adults may converge on an intruder. In isolated pairs, one bird may take charge of leading the young to safety while the other displays toward the intruder.

NESTING

Nests.—Of 86 nests, 69 were on raised sandspits with little or no slope, the remainder on the lower slopes of dunes. Small stones (1–12 cm diameter) were scattered around 31 of 38 nests. Of these, "nearest object" (disregarding vegetation, which would be absent or tiny when nests were initiated) was <0.5 m from one nest and >6 m from 31 nests. In general, nests were not near vegetation on broad beaches but on narrow beaches (as little as 2 m wide) they were sometimes under tufts of marram grass. On extensive tracts of open beach habitat the birds had a wide field of view, and on average left their nests when intruders were 43.1 ± 21.2 m away ($N = 66$, range = 5–93 m). Choice of nest-site in Piping Plovers, in contrast to other Charadrii (Graul 1975), is not tied to proximity of vegetation or physiographic features.

Some Piping Plover nests are lined with fragments of sea shell, accumulated during courtship and incubation. Nests on sand or a sand-gravel surface are unlined, whereas nests on beaches strewn with broken shells are usually lined to some extent. A lining of bleached sea shells increases nest visibility from above, but probably does not aid adults in finding nests, since they normally approach the nest-site on foot. White shell linings are particularly conspicuous in wet weather when the sand color darkens. Three clutches disappeared (lost to predators) from lined nests during heavy rain.

Lining the nest is widespread among plovers. In Red-capped Dotterels the amount of nesting material depends on dampness of the site (Hobbs 1972). Improved drainage due to lining may not be critical to nesting success in Piping Plovers as three watersoaked clutches hatched successfully, suggesting considerable tolerance to moisture.

Egg-laying.—Established pairs court and copulate repeatedly before and during the egg-laying period. Scrapes appeared in territories up to 2 weeks before females selected scrapes and laid first eggs. Copulation and other associated displays fall off rapidly after the clutch is completed, although pair bonds are maintained.

In two cases clutches were completed in 6 days and in one case in 5 days. Intervals between successive eggs ranged from 44–54 h in seven instances, but two intervals were 72 h and 77 h each. These values agree with Wilcox (1959), who reported eggs laid on alternate days, with the clutch completed in 6 days.

Eggs.—The pale buff eggs are marked with fine splotches of black, brownish-black or purplish-black. Markings are usually distributed quite evenly, but some eggs have more, larger, and darker spotting at the broad end. Within clutches intensity and size of markings are usually quite similar.

For 215 eggs from 56 clutches, mean length was 32.5 ± 0.955 mm (range = 29.6–35.4) and mean breadth was 24.8 ± 0.5 mm (range = 23.4–26.1). The mean index of egg volume (length × breadth^2) was 19,927 ± 1054.3 mm^3 (range = 16,486–22,387). A one-way analysis of variance performed on dimensions of the 16 eggs from six clutches whose order of laying in the clutch was known, showed no significant differences ($P \leq 0.05$) among the four clutch positions. However, highly significant differences ($P \leq 0.01$) in dimensions were found among the clutches of individual females.

Piping Plovers raise one brood per year. Mean clutch-size was 3.96 ± 0.2 (N = 68, range = 3–4). Clutches laid later in the breeding season are often smaller and Tufts (1973) suggested that Piping Plovers in Nova Scotia tend to lay fewer eggs in second clutches. The only three 3-egg clutches found were all first clutches.

Incubation.—During the daytime both sexes incubate, probably about equally. In 12.1 h of observations at two nests, females incubated 6.1 h and males 6.0 h. Nest relief involves elements of display and predator distraction. A bird involved in exchanging incubation duties with its mate announces its arrival with one or two notes. The sitting bird usually responds vocally and sometimes also tosses to either side shell fragments from the edge of the nest. The approaching bird always walks to the nest, occasionally shell-tossing. Preferred directions and routes for approaching and leaving are indicated by tracks. At the mate's approach the incubating bird walks from the nest; it too may shell-toss and preen briefly. When being relieved male birds sometimes move away in a low crouched walk similar to the low gliding run of courtship. The relieving bird settles immediately onto the eggs uttering soft throaty peeps. If the departing bird

leaves the territory one or two single peep notes or "peep-low" calls may be given. If the off-duty bird remains it usually squats on the sand some distance from the nest (often at regular sites) closely resembling an incubating bird. Mean time of daytime incubation bouts was 79.4 ± 47.3 min (N = 17, range = 25–153).

When untended nests are filled in with sand, adults use rapid shuffling foot movements to search for eggs, and kick sand away to uncover them. In contrast, Killdeer (Nickell 1943), and Little Ringed and Kentish plovers (Walters 1956) use the bill to locate and uncover buried eggs.

Hatching.—The incubation period (considered here to be time from laying of last egg until hatching of last egg) was 28 days for five clutches, 27 days in one clutch and 29 in another. Two clutches in nests 3 m apart took minimally 31 and 38 days to hatch, because of the greater than normal time devoted to territorial interaction between these adjacent pairs.

Protracted incubation periods for European Oystercatchers (*Haematopus ostralegus*) have been attributed to time adults were kept off the nest by human disturbance (Keighley and Buxton 1948). A case of prolonged incubation period in the Spotted Sandpiper (*Actitis macularia*) (Hays 1972) was attributed to a delay in initiation of steady incubation due to the too close proximity of another nest.

One mateless female Piping Plover incubated her four eggs for a minimum of 39 days before deserting. In contrast, Boyd (1972) and Rittinghaus (1956) reported that widowed female Snowy and Kentish plovers deserted within 4–6 days after the disappearance of a mate.

There was no indication within clutches that eggs laid earlier hatched sooner; most hatched within 4–8 h. However, in a few clutches the hatching period lasted up to 45 h, usually involving delay of only one egg. Eggs failing to hatch were abandoned within 1–2 days. Egg shells are carried on foot up to 40 m from the nest; one bird flew with the shell after walking 10 m.

In 1975, peak hatching occurred during the second and third weeks of June. Probably a number of late June and July hatchings are renests. My observations in 1977, 1978, and 1979 showed peak hatching periods during the third and fourth weeks of June on beaches in New Brunswick, Prince Edward Island, and the Magdalen Islands, where delayed nesting may be related to a longer migration route and the later spring in the Gulf of St. Lawrence. Latest known hatching occurred about 27 July 1977, at Cavendish, P.E.I. The one known nest of a first year bird, a male, contained eggs that hatched 6–8 July 1976.

Out of 25 nests checked on Cadden Beach in 1975, 77 young hatched from 97 eggs, a 79.4% hatching success. Average number of young hatch-

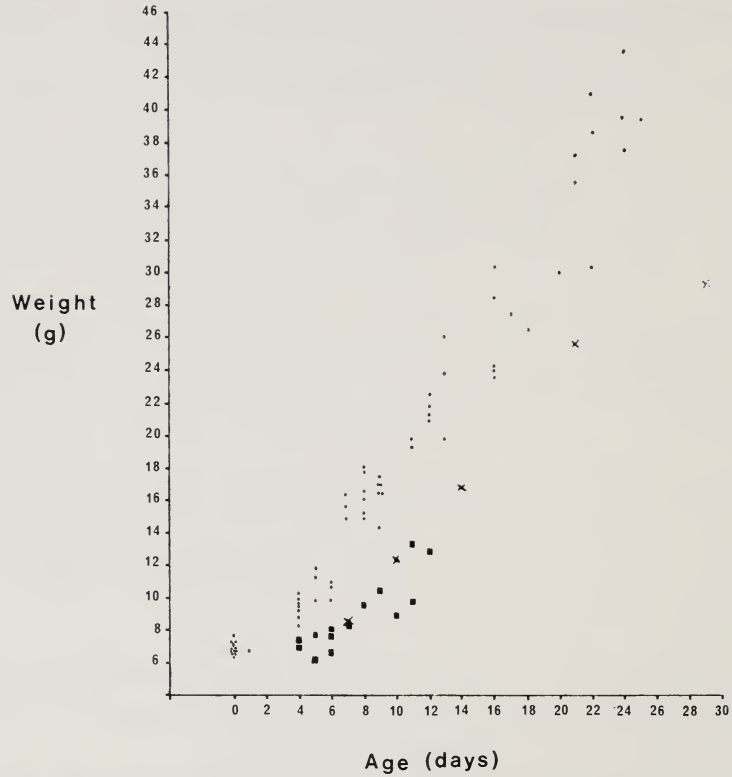


FIG. 4. Weight development of chicks. Dots denote chicks believed to have fledged, squares denote chicks dying before 14 days, and x's indicate values (sample size not reported) given by Wilcox (1959).

ing per nest was 3.08. In 1976, 104 eggs were found in 26 nests of which 75 hatched for a success rate of 72.1% or an average of 2.88 chicks hatched per nest. Of the 49 of 201 eggs which failed to hatch nine were damaged during handling or trapping; 17 were destroyed by mammals or birds (cattle, and probably gulls [*Larus*] or crows [*Corvus*]); and 23 were abandoned in the nest. Wilcox (1959) found somewhat higher success among Long Island Piping Plovers over a 20-year period: 91% hatching, an average of 3.52 young per nest.

Young.—Fig. 4 presents weight development of chicks. Chicks which fail to achieve about 60% of normal weight by day 12 are unlikely to survive. Wilcox (1959) reported chick weights somewhat lower than those obtained on Cadden Beach. Cadden Beach chicks having growth incre-

TABLE 1
PIPING PLOVERS FLOCKING WITH OTHER SPECIES PRIOR TO MIGRATION

	Piping Plovers	Other species (N)	Activity
11 July '75	3 adults	'peep' (112)	feeding
14 July '76	27 adults	Least Sandpiper (110)	feeding
	7 juv.		
15 July '76	12	Least Sandpiper (65)	flying, calling
22 July '76	16	Least Sandpiper (50)	flying, calling
	4	Least Sandpiper (4)	flying, calling
23 July '76	3 adults	Sanderling (3)	feeding
	1 juv.	Semipalmated Sandpiper (2)	
		Least Sandpiper (1)	

ments during their first 10 days as low as those reported by Wilcox (1959) without exception failed to survive.

Two chicks 25 days old could fly >15 m, while two others could fly <2 m. Young of two broods aged 28 and 32 days were flying well. These fledging times are somewhat shorter than the 30–35 days reported by Wilcox (1959).

Fledging success is difficult to assess since older chicks become increasingly elusive. I considered that a chick survived to fledging if when last caught it was known or estimated to be at least 10 days old and exhibited a normal growth pattern at the time (see Fig. 4). The fate of 75 chicks hatching from known nests has been assessed as follows: 29 presumed dead, 28 presumed fledged, and 18 unknown. In addition, at least 11 chicks from nests that were not found are believed to have fledged. Thus, between 39 and 57 chicks may have fledged from Cadden Beach in 1976. This represents approximately 1.3–2.1 chicks fledged per pair. On eight smaller, accessible, recreational beaches 15 pairs fledged between 11 and 17 young or 0.7–1.1 young fledged per pair.

Data on fledging success in other plover species are scarce. For the Ringed Plover fledging rates of one chick per pair (Laven 1940) and 1.28 chicks per pair (Prater 1974) have been reported. Boyd (1962) gave 1.55–2.22 young fledged per pair in Little Ringed Plover and Graul (1975) cited a ratio of one juvenile to three adults in pre-migration flocks of Mountain Plover.

Flocking and departure.—By early July some adults and the oldest of the fledged juveniles increasingly flock on neutral feeding areas and associate with other migrants such as Least Sandpiper (*Calidris minutilla*),

Greater Yellowlegs (*Tringa melanoleucus*), Sanderling (*Calidris alba*), Semipalmated Plover and Spotted Sandpiper (see Table I). Migrating Piping Plovers often give two-note calls while in flight.

SUMMARY

A population of approximately 27–29 pairs of Piping Plovers (*Charadrius melodus*) was studied in southern Nova Scotia in 1975 and 1976. Birds arrived in late April, occupied nesting and feeding territories, and initiated courtship. The aerial display flight of males is similar to that of several other plover species and is used to advertise territorial possession and attract prospective mates. Horizontal threat charges, and ground or aerial chases are used in the establishment of territorial boundaries. Parallel-run displays are more frequently used for boundary maintenance. Scraping, tilt display, and copulatory and distraction behaviors are generally similar to those of other *Charadrius* spp. Mean size of nesting territories was 4000 m^2 and nests averaged about 52 m apart. Of 68 clutches 65 had four eggs and three had three eggs. Most eggs were laid at approximately 48-h intervals; the longest interval was 77 h. Incubation averaged 28 days; one extreme of 38 days was recorded. Egg size varied significantly among females but not with order of laying. Average number of young hatching per nest was 3.08 in 1975 and 2.88 in 1976. Growth rates for most chicks were higher than those reported for birds in New York.

ACKNOWLEDGMENTS

The study was funded in part by a National Research Council of Canada grant to I. A. McLaren at Dalhousie University, where I was supported by a Killam Scholarship. Logistic support was provided by the Nova Scotia Department of Lands and Forests. Financial assistance was received from the Prince Edward Island Department of the Environment for the 1977 and 1978 work and from the Senate Research Committee of the University of P.E.I. in 1979. I thank H. Rueggeberg for assistance in the field, D. Cairns, and J. C. Barlow for critically reviewing the manuscript, and I. A. McLaren for advice and guidance throughout the study.

LITERATURE CITED

Bent, A. C. 1929. Life histories of North American shore birds. Pt. 2. U.S. Natl. Mus. Bull. No. 146.

Boyd, H. 1962. Mortality and fertility of European Charadrii. Ibis 104:368–387.

Boyd, R. L. 1972. Breeding biology of the Snowy Plover at Cheyenne Bottoms Waterfowl Management Area, Barton County, Kansas. MSc. thesis, Kansas State Teachers College, Emporia, Kansas.

Bub, H. 1962. Planberingungen am Sandregenpfeifer (*Charadrius hiaticula*). J. Orn. 103: 243–249.

Cairns, W. E. and I. A. McLaren. 1980. Status of the Piping Plover on the east coast of North America. Am. Birds 34:206–208.

Edwards, G., E. Hosking, and S. Smith. 1947. Aggressive display in the Ringed Plover. Br. Birds 40:12–19.

Glutz von Blotzheim, U. N., K. M. Bauer, and E. Bezzel. 1975. Handbuch der Vogel Mitteleuropas VI (1). Akademische Verlagsgesellschaft. Frankfurt am. Main, Germany.

Graul, W. D. 1973a. Possible functions of head and breast markings in Charadriinae. Wilson Bull. 85:60–70.

———. 1973b. Adaptive aspects of the Mountain Plover social system. Living Bird 12: 69–94.

———. 1975. Breeding biology of the Mountain Plover. Wilson Bull. 87:6–31.

Hall, K. R. L. 1964. A study of the Blacksmith Plover *Hoplopterus armatus* in the Cape Town area. II. Behaviour. Ostrich 35:3–16.

Hays, H. 1972. Polyandry in the Spotted Sandpiper. Living Bird 11:43–57.

Hobbs, J. N. 1972. Breeding of Red-capped Dotterel at Fletcher's Lake, Dareton, N.S.W. Emu 72:121–125.

Keighley, J. and E. J. M. Buxton. 1948. The incubation period of the Oystercatcher. Br. Birds 61:261–266.

Laven, H. 1940. Beitrage zur Biologie des Sandregenpfeifers (*Charadrius hiaticula* L.). J. Orn. 88:183–287.

Lenington, S. and T. Mace. 1975. Mate fidelity and nesting site tenacity in the Killdeer. Auk 92:149–151.

Maclean, G. L. 1972. Problems of the display postures in the Charadrii (Aves: Charadriiformes). Zool. Afric. 7:57–74.

Mason, A. G. 1947. Territory in the Ringed Plover. Br. Birds 40:12–19.

Nickell, W. P. 1943. Observations on the nesting of the Killdeer. Wilson Bull. 55:23–28.

Phillips, R. E. 1972. Sexual and agonistic behavior in the Killdeer (*Charadrius vociferus*). Anim. Behav. 20:1–9.

Prater, A. J. 1974. Breeding biology of the Ringed Plover *Charadrius hiaticula*. Pp. 15–22 *in* Proc. IWBR Wader Symposium, Warsaw, Poland.

Rittinghaus, H. 1956. Untersuchungen am Sandregenpfeifer (*Charadrius alexandrinus* L.) auf der Insel Oldeoog. J. Orn. 97:117–155.

Simmons, K. E. L. 1953a. Some studies on the Little Ringed Plover. Avic. Mag. 59:191–207.

———. 1953b. Some aspects of the aggressive behaviour of three closely related plovers (*Charadrius*). Ibis 95:115–127.

———. 1956. Territory in the Little Ringed Plover *Charadrius dubius*. Ibis 98:390–397.

Sluiters, J. E. 1938. Bijdrage tot de biologie van den Kleinen Plevier (*Charadrius dubius curonicus* Gm.). Ardea 27:123–151.

Spencer, K. G. 1953. The Lapwing in Britain. A. Brown and Sons, London, England.

Sutton, G. M. and D. F. Parmelee. 1955. Breeding of the Semi-palmated Plover on Baffin Island. Bird-Banding 26:137–147.

Tomkins, I. R. 1944. Wilson's Plover in its summer home. Auk 61:259–269.

Tufts, R. W. 1973. The birds of Nova Scotia. Nova Scotia Museum, Halifax, Nova Scotia.

Walters, J. 1956. Eiruckgewinnung und Nistplatzorientierung bei See- und Flussregenpfeifer (*Charadrius alexandrinus* und *dubius*). Limosa 29:103–129.

Wilcox, L. 1939. Notes on the life history of the Piping Plover. Birds of Long Island, No. 1:3–13. Bird Club of Long Island, Long Island, New York.

———. 1959. A twenty year banding study of the Piping Plover. Auk 76:129–152.

Witherby, H. F., F. R. C. Jourdain, N. P. Ticehurst, and B. W. Tucker. 1965. The handbook of British Birds. Vol. IV. London, England.

BIOLOGY DEPT., DALHOUSIE UNIV., HALIFAX, NOVA SCOTIA B3H 4J1, CANADA. (PRESENT ADDRESS: 60 NEWLAND CRES., CHARLOTTETOWN, PRINCE EDWARD ISLAND C1A 4H7, CANADA.) ACCEPTED 22 APR. 1982.

Wilson Bull., 94(4), 1982, pp. 546–550

GENERAL NOTES

Comparison of variable circular-plot and spot-map methods in desert riparian and scrub habitats.—Accurately censusing bird populations has been a major concern of avian ecologists for many years (Kendeigh, Ecol. Monogr.14:67–106, 1944; Enemar, Var Fagelvarld Suppl. 2, 1959; Berthold, J. Orn. 117:1–69, 1976). Two methods are in extensive use in the United States: (1) the spot-map method (referred to as SMM) (Williams, Ecol. Monogr. 6:317–408, 1936) and (2) the variable-width transect method (Emlen, Auk 88:323–342, 1971; Emlen, Auk 94:455–468, 1977). Transects, spot-mapping, and point counts are heavily used in European countries (Blondel et al., Alauda 389:55–71, 1970; Järvinen and Väisänen, Oikos 26:316–322, 1975; Bournaud and Corbille, Terre Vie Rev. Ecol. 33:71–94, 1979). Most methods present problems in censusing small discrete areas of habitat.

In most riparian situations in the southwest it is difficult to find areas of homogeneous vegetation either 1–1.5 km in length for transects and/or greater than 10 ha in size for a SMM grid. Spot-mapping is also limited to the breeding season when the birds are defending and holding territories. Point counts are useable in small habitat "islands," but they fail to define the area censused.

Reynolds et al. (Condor 82:309–313, 1980) have recently proposed a variable circular-plot method (referred to as VCPM) that should be useful for counting birds in small habitat patches. With this method birds are counted around selected points; the distance from each point to the bird is estimated, which permits results to be expressed in terms of number of birds per unit area. This method would be useful in riparian situations in the southwest as well as other small areas of habitat, particularly if it could be demonstrated that it produces results comparable to the more established methodologies. Ideally, the method should be comparable both in riparian and in adjacent areas which might affect bird community structure in riparian habitats (Carothers et al., Am. Zool. 14:97–108, 1974; Szaro, pp. 403–418 *in* Management of western forests and grasslands for nongame birds, R. M. Degraff, tech. coord., USDA For. Serv. Gen. Tech. Rept. INT–86, Ogden, Utah, 1980). The purposes of this study, therefore, were (1) to assess the applicability of the VCPM to riparian and desert scrub habitats, and (2) to assess the comparability of the VCPM to the SMM.

Study areas.—The study was conducted on the Tonto National Forest, on Queen Creek, about 3.7 km upstream from the mouth of Whitlow Canyon and about 16 km west of Superior, Pinal Co., Gila River Basin, Arizona. We selected two study plots, one in a riparian area at 620 m elevation and the other in the adjacent desert scrub at 630 m elevation. The riparian plot, located immediately behind Whitlow Ranch Dam, was 250 × 450 m minus a 100 × 100-m square in the northwest corner (10.25 ha). The adjacent desert scrub plot was a 400 × 400-m square (16.0 ha). Both plots were gridded in a pattern of 50-m squares. The riparian area consisted of approximately 15 ha with a central core of even-aged Goodding willow (*Salix gooddingii*) surrounded by dense salt cedar (*Tamarix pentandra*) thickets. The desert plot was dominated by foothill paloverde (*Cercidium microphyllum*) and saguaro cactus (*Cercus giganteus*).

Methods.—Breeding bird counts were made using both the SMM (Kendeigh 1944) and the VCPM (Reynolds et al. 1980). For the SMM, nine visits were made to each plot from 15 April–29 June 1980. For the VCPM, four visits were made to each plot from 8 May–5 June 1980. For the VCPM, 14 stations were selected (within the grid pattern) in both habitats so that each point was at least 100 m from the nearest point. During the period when both methods were used, sampling was done on consecutive days with the order reversing for each sequence. Consecutive SMM counts began at opposite ends of the study areas. Similarly, VCPM counts began at stations 1 or 14. All counts began at approximately 06:20.

For the VCPM, the observer waited at each point for a 1-min "rest period" to allow for equilibration of bird activity. During the 8-min count period recommended by Reynolds et al. (1980) for closed canopy forests, the observer recorded all birds seen or heard and their distances from the point. Distances were determined with the aid of an optical rangefinder. Bird densities were plotted for each 5-m band from 0–100 m from the point and for each 10-m band from 100–200 m from the point. The inflection point was determined by choosing the edge of band where density of individuals of a given species in the next outermost band was less than 50% of the previous band. The effective detection distance, the distance from the center point to the inflection point, was determined by pooling all observations for a species within a habitat type over the entire sampling period. Individual point densities for each species for the entire study period were then determined using this effective detection distance. Mean species-densities and standard errors for each study plot were then calculated from the individual point densities.

Density estimates were determined for all species with a minimum of 10 records during the study period. The number of singing males and "all other observations" were recorded separately (Emlen 1971). The density of singing males was then doubled to account for the females of the territorial males unless that number was less than the number of singing males plus the number of "all other observations." In the latter case the total number of observations was used for density purposes (Franzreb, Condor 78:260–262, 1976; Reynolds et al. 1980). In our study all densities were determined with the total number of observations except for those of the Cardinal (see Table 1 for scientific names), Bell's Vireo, and Yellow-breasted Chat on the riparian plot only which were determined by doubling the number of singing males.

Results.—Density estimates from the SMM for all species except the White-winged Dove on the riparian area were within the 95% confidence limits around the mean for the VCPM estimates (Table 1). Total density for the 13 species nesting on the riparian area estimated by the VCPM was 323 pairs/40 ha, compared to the estimate of 388 pairs/40 ha for the same species by the SMM. In the desert scrub habitat, the total density estimate, again for 13 species, was 98 pairs/40 ha by the VCPM and 105 pairs/40 ha by the SMM. All SMM density estimates on the desert plot were within the 95% confidence limits for the VCPM estimates.

Total effort expended for the SMM was 34.5 h on the riparian area and 32.5 h on the desert scrub area divided among nine visits to each plot. Total effort expended (count and equilibration periods plus walking time) for the VCPM estimate was 13.5 h on the riparian area and 10.8 h on the desert scrub area divided among four visits to each plot. The actual time spent counting (8 min × 14 stations × 4 visits) was 7.5 h on both areas using the VCPM.

Discussion.—The close agreement in density estimates determined from the two methods shows the potential of the VCPM for censusing bird populations in small habitat "islands." The density estimates were significantly different for only one species, the White-winged Dove that maintains a Type B territory (Nice, Am. Midl. Nat. 26:441–487, 1941).

The agreement in density estimates between methods tested here would probably increase with an increased VCPM sample for the rarer species. There were minimal differences (less than 17%) in density estimates for the most abundant species (Lucy's Warbler, Abert's Towhee, Black-throated Sparrow, Yellow Warbler). These species were also the most frequently observed during the VCPM counts. Reynolds et al. (1980) showed that a species' abundance and distribution (variably or uniformly distributed) will affect the number of stations and/or visits required to count a species adequately. To maximize the number of density estimates, such estimates were calculated for all species that were observed 10 times or more in either the riparian or desert areas. However, only the Ash-throated Flycatcher, Wied's Flycatcher, Gila Woodpecker, and Abert's Towhee, all on the desert plot, were estimated with fewer than 15 observations.

Table 1

Breeding Bird Densities (pairs/40 ha) in Goodding Willow-Salt Cedar and Paloverde-Saguaro Associations Determined by Both the Variable Circular-Plot and Spot-Map Methods

Species	Riparian plot		Desert scrub plot	
	Variable circle	Spot-map	Variable circle	Spot-map
Gambel's Quail (*Lophortyx gambelii*)	—	—	10 ± 1.2	9
White-winged Dove (*Zenaida asiatica*)	44 ± 7.4[a]	70	7 ± 1.9	10
Mourning Dove (*Zenaida macroura*)	15 ± 5.3	23	7 ± 2.0	10
Black-chinned Hummingbird (*Archilochus alexandri*)	21 ± 5.0	20	7 ± 2.9	5
Gila Woodpecker (*Centurus uropygialis*)	—	—	3 ± 1.2	3
Ladder-backed Woodpecker (*Picoides scalaris*)	11 ± 4.0	12	N.E.[b]	2
Wied's Crested Flycatcher (*Myiarchus tyrannulus*)	9 ± 4.4	15	6 ± 3.2	5
Ash-throated Flycatcher (*Myiarchus cinerascens*)	—	—	4 ± 1.2	4
Verdin (*Auriparus flaviceps*)	—	—	10 ± 5.8	7
Cactus Wren (*Campylorhynchus brunneicapillus*)	—	—	5 ± 2.6	6
Bell's Vireo (*Vireo bellii*)	8 ± 2.5	9	N.E.	1
Lucy's Warbler (*Vermivora luciae*)	109 ± 12.9	125	11 ± 3.4	15
Yellow Warbler (*Dendroica petechia*)	24 ± 7.3	29	—	—
Yellow-breasted Chat (*Icteria virens*)	19 ± 3.8	16	N.E.	1
Brown-headed Cowbird (*Molothrus ater*)	13 ± 5.8	12	N.E.	4
Summer Tanager (*Piranga rubra*)	10 ± 3.8	10	—	—
Cardinal (*Cardinalis cardinalis*)	10 ± 4.6	12	5 ± 1.7	5

TABLE 1
CONTINUED

Species	Riparian plot		Desert scrub plot	
	Variable circle	Spot-map	Variable circle	Spot-map
Abert's Towhee (*Pipilo aberti*)	30 ± 7.4	35	5 ± 2.2	5
Black-throated Sparrow (*Amphispiza bilineata*)	—	—	18 ± 6.2	16
Total density	323	388	98	105
Species richness	13	19[c]	13	22[c]

[a] Mean density ± SE.
[b] Species observed but not enough data for a density estimate.
[c] Includes all species, i.e., those not estimated by both methods on a single site.

We found the VCPM underestimated total bird density as compared to the SMM by 17% on the riparian plot and by 7% on the desert plot. In contrast to DeSante (Stud. Avian Biol. 6:177–185, 1981), all bird densities in our study were not underestimated by the VCPM. On the riparian plot, the Yellow-breasted Chat, Brown-headed Cowbird, and Black-chinned Hummingbird had higher densities with the VCPM. On the desert plot we found an even distribution of our estimates with four species underestimated, five species overestimated, and four species with no difference in density (Table 1).

All species recorded by the SMM were also observed during the VCPM sampling. However, ten were not observed with high enough frequencies during VCPM sampling to calculate a density estimate. For less common and rare species, the VCPM may require as many sampling periods as the SMM for density estimation. For common species, the method requires substantially fewer visits to an area to obtain comparable density estimates.

However, once an effective detection distance for a rarer species is determined in a given habitat type, the number of sampling visits necessary to calculate density estimates for these species would decrease. Thus, repeated sampling of the same site in subsequent years by the VCPM would require substantially fewer visits than by the SMM.

The determination of band size is potentially a problem in the use of the VCPM. As suggested by Reynolds et al. (1980), band width should be 5-m widths from 0–100 m, and 10-m widths from 100–200 m from the station. DeSante (1981) used 30-foot bands from 0–600 feet and then 60-foot bands from 600–1200 feet. Anderson and Ohmart (Stud. Avian Biol. 6:186–192, 1981) recommended that the first band have a width of 30 m. This recommendation might be useful in the more open habitats along the lower Colorado River but in our dense riparian habitat the effective detection distance averaged only 37.3 ± 3.5 m. If we had used a first band of 30 m then for most species we would have used only the first and second bands in our density determinations. We feel that band width probably should be determined by habitat density.

Distance estimation is the major factor affecting accurate bird-density estimates with both the VCPM and line transect methods. The bias in density estimates from measurement errors can be reduced by training observers, flagging known distances, and using rangefinders (Scott et al., Stud. Avian Biol. 6:334–340, 1981). We had the advantage of having a previously gridded SMM plot to use as a guide for distance estimation. However, the flagging of a few

known distances from each point should not require any more effort than setting up a SMM grid.

The VCPM has the same advantage over the SMM as Emlen's (1971) line transect method, that of being applicable for year-round studies. It has the added advantage of eliminating the bias involved in estimating the sighting angles needed for line transect density estimates (Burnham et al., Wildl. Monogr. 72:2–202, 1980). Moreover, the VCPM combines the usefulness of point counts in small habitats while defining the area censused.

We thank Bertin Anderson, Rudy King, Ralph Raitt, Richard Reynolds, Jared Verner, and Robert Whitmore for comments on this note.—Robert C. Szaro and Martin D. Jakle, *U.S.D.A. Forest Service, Rocky Mountain Forest and Range Experiment Station. Arizona State Univ., Tempe, Arizona 85287.* *Accepted 16 June 1982.*

Wilson Bull., 94(4), 1982, pp. 550–554

Use of prairie wetlands by selected bird species in South Dakota.—Most studies of prairie wetlands have concentrated on waterfowl; however, wetland habitat in the prairies is also important to other kinds of birds. Our purpose is to report use of natural and man-made wetlands by 13 selected bird species other than waterfowl to provide information useful for management of these wetland birds, as well as for management of prairie wetlands. Quantification of the use of wetlands by all avian species will allow managers a more comprehensive view of the importance of such areas.

Study area and methods.—We surveyed sample wetlands within 476 legal quarter-sections (0.65 km^2) chosen by a combination of stratified random and two-stage cluster sampling (Steel and Torrie, Principles and Procedures of Statistics, McGraw-Hill Co., Inc., New York, New York, 1960). Study plots and wetlands were representative of South Dakota, exclusive of the Black Hills region. A detailed description of the study area and sampling scheme was presented in Brewster et al. (J. Wildl. Manage. 40:50–59, 1976).

Wetland birds were censused from 12–24 May and 10–21 June 1975 and from 10–23 May and 7–12 June 1976. Censuses were conducted by three two-person teams equipped with binoculars and waders. Counts were made from 30 min after sunrise until 30 min before sunset.

Selection of target species for inclusion in the study was based on anticipated abundance of a species on the study areas and the ease with which species could be observed and censused. Species selected for study included Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*), Red-winged Blackbird (*Agelaius phoeniceus*), Lesser Yellowlegs (*Tringa flavipes*), Marbled Godwit (*Limosa fedoa*), Willet (*Catoptrophorus semipalmatus*), American Avocet (*Recurvirostra americana*), American Bittern (*Botaurus lentiginosus*), Black Tern (*Chlidonias niger*), Great Blue Heron (*Ardea herodias*), Black-crowned Night-Heron (*Nycticorax nycticorax*), Green-backed Heron (*Butorides striatus*), Wilson's Phalarope (*Phalaropus tricolor*), and Sora (*Porzana carolina*).

The total number of individuals seen of each species was recorded for each wetland visited. Only territorial male Yellow-headed and Red-winged blackbirds were counted because of the inconspicuousness of the females of these species. Of the target species, the Sora was the most difficult to census. Based on densities of Soras observed in other studies (Pospichal and Marshall, Flicker 26:2–32, 1954; Griese et al., Wilson Bull. 92:96–102, 1980), we believe our counts recorded only a small percentage of those present. Use of taped calls to census rails was not feasible due to the extensive area covered in our survey, the necessity of simultaneously censusing waterfowl, and limited manpower.

Natural wetlands were classified using the method of Stewart and Kantrud (U.S. Fish Wildl. Serv. Resour. Publ. 92:1–57, 1971). Fluviatile wetlands were categorized as intermittent or permanent streams. Intermittent streams were defined as stream channels with intermittent pools of water but without continuous flowing water during censusing. Man-made wetlands were classified as stock ponds (ponds formed by construction of earthen dams across natural waterways), and dugouts (excavated ponds about 0.1 ha in size). Wetlands with tilled soil bottoms or wetlands in pastures and without aquatic vegetation were classified as tillage and pasture ponds, respectively. In the absence of tillage or grazing, most such wetlands would have been classed as ephemeral or temporary ponds.

Results and discussion.—Glacial ponds and fluviatile wetlands constituted 49% of the wetlands surveyed (excluding dry basins) and 67% of the total surface water area. Man-made wetlands represented 47% of the wetlands surveyed and 25% of the total surface water area. Stock ponds and dugouts were the predominant man-made wetlands encountered in the survey.

Each of the target species occurred most frequently on one of the natural wetland types. Five target species were most frequently recorded on semipermanent ponds, three on permanent streams, two each on temporary ponds and ephemeral ponds, and one on seasonal ponds (Table 1). Overall, 78% of the semipermanent ponds surveyed had one or more of the target species present, the highest count of all wetland types surveyed (Table 2). Red-winged and Yellow-headed blackbirds, Soras, American Bitterns, and Black Terns all had their highest frequency of occurrence on semipermanent ponds. In northern Iowa, greatest density and diversity of marsh birds were associated with an interspersion of half emergent vegetation and half open water on marshes (Weller and Fredrickson, Living Bird 12:269–291, 1973). Among the wetland types we observed, semipermanent wetlands best exemplified the combination of open water and emergent vegetation described by Weller and Fredrickson (1973).

One or more of the target species occurred on 65% of the permanent streams and on 61% of the intermittent streams (Table 2). The Black Tern was the only species not observed on either permanent or intermittent streams. Great Blue, Black-crowned Night, and Green-backed herons occurred most frequently on permanent streams. Frequencies of Great Blue Herons on permanent streams greatly exceeded those on intermittent streams. Black-crowned Night-Herons were not found on intermittent streams. Yellow-headed Blackbirds, Wilson's Phalaropes, Marbled Godwits, and Willets were recorded on intermittent streams but not on permanent streams. Wilson's Phalaropes have been observed along the Big Sioux River, a permanent stream, during spring flooding in April.

With the exception of Great Blue and Green-backed herons all of the target species observed on semipermanent ponds also occurred on seasonal ponds (Table 1). Wilson's Phalaropes occurred most frequently on seasonal ponds. The frequency of Sora and Yellow-headed Blackbird occurrence on these ponds was exceeded only by that on semipermanent ponds.

All of the target species, with the exception of Green-backed Herons, used stock ponds (Table 1); and nearly half of the stock ponds had one or more target species present (Table 2). Marbled Godwit, Wilson's Phalarope, Black Tern, and Great Blue Heron frequencies on stock ponds were second only to one other wetland type. With the exception of the Green-backed Heron, all target species observed on semipermanent ponds were also observed on stock ponds. Habitat variation was minimal because stock ponds were generally deeper than natural wetlands, and emergent vegetation was either limited to littoral zones or absent. Some silted-in stock ponds with extensive shallow water (<1 m in depth) combined areas of emergent vegetation interspersed with open water as was characteristic of many semipermanent ponds.

Table 1

Frequency of Occurrence[a] by Wetland Classification of Selected Bird Species Recorded During May and June Surveys in South Dakota, 1975–1976

Species	Wetland class[b] and no. wetlands sampled								
	Semi-permanent ponds (256)	Stock ponds (378)	Intermittent streams (334)	Seasonal ponds (266)	Dugouts (452)	Permanent streams (91)	Temporary ponds (73)	Tillage and pasture ponds (91)	Ephemeral ponds (20)
Red-winged Blackbird	74.2	38.9	59.3	51.9	19.9	52.7	37.0	6.6	—
Yellow-headed Blackbird	37.5	5.6	2.4	6.8	0.7	—	2.7	1.1	—
Wilson's Phalarope	7.4	8.7	3.0	9.8	1.8	—	8.2	2.2	5.0
Lesser Yellowlegs	1.6	2.1	0.9	1.9	0.9	2.2	2.7	—	—
Marbled Godwit	2.3	2.4	1.5	1.5	1.5	—	4.1	1.1	—
Willet	4.7	2.6	1.2	3.4	1.1	—	4.1	—	5.0
Sora	5.5	0.8	2.1	3.4	0.2	2.2	—	—	—
American Bittern	6.3	0.5	1.2	0.8	0.2	1.1	—	—	—
American Avocet	—	0.8	0.3	0.4	0.2	1.1	1.4	6.6	10.0
Black Tern	6.3	3.2	—	1.1	0.2	—	—	—	—
Great Blue Heron	1.2	2.1	0.3	—	—	12.1	—	—	—
Black-crowned Night-Heron	1.2	0.8	—	0.4	—	3.3	—	—	—
Green-backed Heron	0.4	—	0.3	—	—	5.5	—	—	—

[a] Percentage of the total number of wet basins surveyed in each wetland class with a particular bird species present.
[b] Definition of glacial pond types according to Stewart and Kantrud (1971).

Table 2

Percentile Distribution of Each Wetland Category Based on Numbers of Wetland Bird Species (Target Species) Recorded

Number of species recorded	Wetland categories								
	Stock ponds (378)[a]	Semi-permanent ponds (256)	Seasonal ponds (266)	Inter-mittent streams (334)	Permanent streams (91)	Temporary ponds (73)	Dugouts (452)	Ephemeral ponds (20)	Tillage and pasture ponds (91)
1	29.1[b]	31.3	36.5	51.2	42.9	30.1	23.2	10.0	13.2
2	12.7	25.0	13.5	6.6	16.5	6.8	2.2	15.0	2.2
3	2.6	14.1	3.4	1.8	4.4	6.8	0.4	—	—
4	1.1	6.3	1.5	0.6	1.1	—	—	—	—
5	0.8	1.2	0.4	0.6	—	—	—	—	—
6	0.8	—	—	—	—	—	—	—	—
7	—	—	—	—	—	—	—	—	—
8	—	—	—	—	—	—	—	—	—
9	—	—	—	—	—	—	—	—	—
10	0.3	—	—	—	—	—	—	—	—
Total	47.4	77.9	54.8	60.8	64.9	43.7	25.8	25.0	15.4

[a] The total number of wet basins surveyed in each category.
[b] The percentage of the total number of wet basins.

Only 26% of the dugouts had one or more target species present. However, all of the target species with the exception of the three heron species occurred on dugouts. We observed some Great Blue Heron use of dugouts outside of the study plots. The small size ($\bar{x}$ = 0.10 ha), depth ($\bar{x}$ < 2 m), and steep shoreline slope of most dugouts precluded extensive growth of emergent vegetation. Also, many dugouts were completely devoid of emergent vegetation due to intensive use by cattle. Steep shoreline slopes may discourage use by wading birds.

Temporary and ephemeral ponds persisted only a short time following cessation of snowmelt and spring rains. This fact, coupled with the drought conditions that prevailed during the study, reduced the availability of these wetland types. Under more typical conditions, however, the periodic drying and flooding regime of such ponds favors high populations of aquatic invertebrates (Krapu, Auk 91:278–290, 1974) which may account for the peak frequency of occurrence of Lesser Yellowlegs and Marbled Godwit on temporary ponds and of Willet and American Avocet on ephemeral ponds.

Tillage and pasture ponds were typically small in size with little or no emergent vegetation and were the least likely of all wetland types to have a target species present (Table 2). However, the frequency of occurrence of American Avocet on tillage and pasture ponds was only exceeded by its occurrence on ephemeral ponds (Table 1). Disturbance of shallow wetlands by intensive grazing or tillage appears to discourage use by most wetland birds.

Implications.—The diversity of wetland types in the northern great plains is important to a variety of avian species other than waterfowl. Considerable loss of glacial wetlands has occurred in the northern prairies due to drainage (National Academy of Sciences, Special Problems of Waters and Watersheds, pp. 149–180 *in* Land Use and Wildlife Resources, National Research Council, Washington, D.C., 1970) and drainage continues at a rapid pace. Shallow ephemeral and temporary wetlands are especially vulnerable to drainage. Drainage

of shallow wetlands may affect not only breeding waterfowl (Krapu, Auk 91:278–290, 1974), but other avian species such as Lesser Yellowlegs, Marbled Godwit, Willet, and American Avocet. Other less abundant or difficult to census species not included in our study may be among those most severely affected by drainage. The widespread drainage of private wetlands, including semipermanent ponds and lakes, threatens habitat important to a variety of bird species that either migrate through or nest in the northern great plains.

Acknowledgments.—We thank Harold F. Duebbert and Raymond L. Linder for critically reviewing this manuscript and W. Lee Tucker for providing advice on sampling design. Financial support for this study was provided by the South Dakota Agricultural Experiment Station (Project H–615) and the South Dakota Water Resources Institute (Project A–038–SDAK and B–045–SDAK). This paper was approved for publication by the Director, Agricultural Experiment Station, South Dakota State University, as Journal Series No. 1748.—Michael J. Weber, *U.S. Forest Service, P.O. Box 194, Idabel, Oklahoma 74745*; Paul A. Vohs, Jr., *U.S. Fish and Wildlife Service, 18th and C Streets, N.W., Washington, D.C. 20240*; and Lester D. Flake, *Dept. Wildlife and Fisheries Sciences, P.O. Box 2207, South Dakota State Univ., Brookings, South Dakota 57007.* *Accepted 15 Feb. 1982.*

Wilson Bull., 94(4), 1982, pp. 554–555

Sexing Saw-whet Owls by wing chord.—Weir et al. (Wilson Bull. 92:475–488, 1980) present an analysis of the fall migration of Saw-whet Owls (*Aegolius acadicus*) at Prince Edward Point, Ontario. All owls with a wing chord ≤134 mm were designated males and all with wing chord ≥141 mm females. Those between 134 and 141 mm were classed as sex unknown (U). This method led to an unbelievable preponderance of identified males in the juvenile (HY) age class (Table 1). It seems grossly unlikely that juvenile males are extremely more abundant than females at Prince Edward Point because the sex ratio of identified adults (PHY) does not differ significantly from unity (Table 1). It is probable that the juveniles are not being sexed properly.

The sexing method is apparently based on the study of Earhart and Johnson (Condor 72: 251–264, 1970) who measured museum specimens and found a mean wing chord of 132.2 ± 3.83 mm for males and 139.2 ± 2.45 mm for females. The limits used by Weir et al. (1980) are approximately at the 95% confidence intervals from the means of Earhart and Johnson (1970) and thus should be a reasonable estimator of sex. However, Earhart and Johnson (1970) did not determine the age of their specimens and Mueller and Berger (Bird-Banding 38:120–125, 1967) have shown that juvenile Saw-whet Owls have significantly shorter wing chords ($\bar{x}$ = 136.5 mm) than adults ($\bar{x}$ = 138.5 mm). This age difference is 29% of the difference between means for the sexes given by Earhart and Johnson (1970) and 33% of the gap between sexes in the sexing method used by Weir et al. (1980). Mueller and Berger (Auk 85:431–436, 1968) have suggested that measurements of museum specimens may be shorter than those taken from live birds because of possible shrinkage in drying. Mueller et al. (Bird-Banding 47:310–318, 1976) have indicated that measurements probably vary with the method of measurement. Thus, it is not surprising that a further examination of the data of Mueller and Berger (1967), using the sexing method of Weir et al. (1980), yields a biased sex ratio for sexed adults but not for sexed juveniles (Table 1), the opposite of that found by Weir et al. (1980). A further caveat: an examination of the distribution of measurements used in Mueller and Berger (1967) reveals that an average difference of measurement of only 1 mm (0.8% of wing chord), due to slight, but reasonably consistent differences in measuring techniques, would change the sex identification of 11–14% of their sample from identified to unidentified or vice versa, but not from male to female. A 2-mm difference (1.5%) would similarly change the sex identification of 24–31%.

Table 1
Sex Ratios of Saw-whet Owls[a]

Year	HY males	HY females	U	χ^2	P
1976	46	16	35	14.5	<0.0002
1977	187	84	118	39.2	<0.0001
1978	54	23	46	12.5	<0.0005
Total	287	123	199	65.6	<0.0001
M and B	43	30	27	2.3	>0.10
Year	PHY males	PHY females	U	χ^2	P
1976	36	30	26	0.6	>0.45
1977	62	49	52	1.6	>0.20
1978	55	57	68	0.0	>0.95
Total	153	136	146	1.0	>0.30
M and B	16	30	22	4.3	<0.05

[a] Data from Weir et al. (1980) except for M and B which are from the sample used in Mueller and Berger (1967). Chi-square compares observed values with a 1:1 sex ratio.

Edwards, Weir and Stewart (Wilson Bull. 94:555–557, 1982) present calculations which suggest that if one considers the proportions of males and females in the unidentified category, the sex ratio of the total sample does not differ from unity. Their analysis evades the central issue of age differences by combining the age groups. If we use their estimates of the proportion of unidentified birds that are males (29%) and females (71%), apply this separately to the two age groups, and add the numbers of birds that were sexed, we obtain the following: HY: males—345, females—264, $P < 0.002$; PHY: males—195, females—240, $P < 0.04$. We have, thus, significantly biased sex ratios in both HY and PHY. This strongly suggests that the sexing method of Weir et al. (1980) is not sufficiently accurate for either age group.

We need data from a sufficient sample of known-age, known-sex Saw-whet Owls to establish a reasonable estimate of the true means, standard deviations, and hence the 95% confidence intervals for determining sex. The method of measurement should be described in detail. At present, we do not know the accuracy of the sexing method used by Weir et al. (1980).

Weir et al. (1980) conclude that Saw-whet Owls show sexual differences in the timing of migration. On the basis of the evidence presented above, it appears that their conclusions may be inconclusive.—Helmut C. Mueller, *Dept. Biology and Curriculum in Ecology, Univ. North Carolina, Chapel Hill, North Carolina 27514.* *Accepted 20 July 1982.*

Wilson Bull., 94(4), 1982, pp. 555–557

Comments on sexing Saw-whet Owls by wing chord.—Mueller (Wilson Bull. 94:554–555, 1982) feels it unbelievable that there are more identified males than identified Saw-whet Owl (*Aegolius acadius*) females in the work by Weir et al. (Wilson Bull. 92:475–488, 1980). However, it is entirely expected from the data of Earhart and Johnson (Condor 72:251–264,

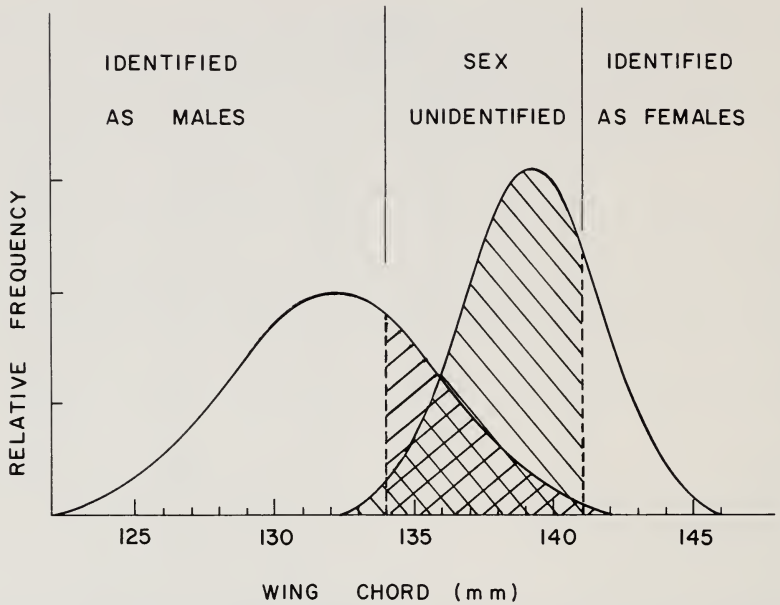


FIG. 1. Identification of sex of Saw-whet Owls, assuming normal distribution of male and female wing chords (Earhart and Johnson 1970), males 132.2 ± 3.83 mm, females 139.2 ± 2.45 mm.

1970), assuming a normal (Gaussian) sample population of males and females (mean wing chord of 132.2 ± 3.8 mm for males and 139.2 ± 2.4 mm for females).

Shown in Fig. 1 are the normal curves for these distributions together with the cut-off limits (wing chord ≤134 mm for males and ≥141 for females). The area under the curve to the left of 134 mm represents the fraction of the total population of males that can be identified and the area under the curve to the right of 141 mm represents the fraction of the total population of females that can be identified. This procedure permits 68% of the males to be identified as males and 23% of the females to be identified as females. We therefore expect to fail to identify more females (77%) than males (32%). Thus, the unidentified (U) category is expected to contain 29% males (i.e., 32/[32 + 77]) and 71% females (77/[32 + 77]). The essence of Mueller's (1982) misconception is that he expected equal fractions of males and females to be identifiable.

One can, in fact, calculate the numbers of males and females expected in the unidentifiable category by assigning sex as 29% males and 71% females. Such an assignment for the 345 unidentified birds in the data of Weir et al. (1980) as listed in their Table 2 and included in Mueller's (1982) Table 1 (above) leads to an overall total (HY and PHY) for 1976, 1977, and 1978 of 531 males, 503 females, or 51% male, 49% female. This is clearly not far from expectation of equal fractions in the overall population.

Weir et al. (1980) were anxious not to misidentify as to sex hence the conservative criteria used (only 1.7% of the females should have wing chords ≤134 mm, and only 1.1% of the males ≥141), and the inclusion of the unidentified category. Their analysis clearly stated that the findings related to timing of migration apply to the owls of known sex.

Mueller is of course correct that there are small age-dependent size differences between HY and PHY birds. Including such age difference would split each of the peaks in the unaged distribution shown in Fig. 1 into two peaks, but consistent data were not available to us at the time of writing. We have been acquiring such data ourselves, and have measured 2588 birds to date. Our statistical analysis (unpubl.) yields mean wing chords of 131.8 ± 3.6 mm for HY males, 133.1 ± 3.3 mm for PHY males, 139.3 ± 3.6 mm for HY females, and 140.8 ± 3.3 mm for PHY females. Clearly, the age-dependent differences of 1.3 mm for males and 1.5 mm for females are much smaller than the sex-dependent differences of 7.4 mm for HY birds and 7.7 mm for PHY birds.—Martin H. Edwards, *Dept. Physics*, Ron D. Weir, *Dept. Chemistry and Chemical Engineering, Royal Military College of Canada, Kingston, Ontario K7L 2W3, Canada*, and Robert B. Stewart, *Dept. Microbiology, Queen's Univ., Kingston, Ontario K7L 3N6, Canada.* *Accepted 27 July 1982.*

Wilson Bull., 94(4), 1982, pp. 557–564

Use of two habitats related to changes in prey availability in a population of Ospreys in northeastern Nova Scotia.—Reproductive success of altricial birds may depend largely on the ability of adults to find and bring sufficient food from foraging sites to their nestlings. In particular, large raptorial birds that forage for seasonally fluctuating and patchily distributed prey may encounter problems in obtaining enough food for both themselves and the rearing of their young. Presumably the feeding and nesting strategies developed by a species reflect the abundance, distribution, and availability of prey for the predator.

Time budget studies of nest-site activities of Ospreys (*Pandion haliaetus*) have been limited (Green, Ibis 118:475–490, 1976; Stinson, Oecologia 36:127–139, 1978; Levenson, M.S. thesis, Humboldt State Univ., Arcata, California, 1976). Even today relatively little is known about details of Osprey nesting activity, especially relative differences in time budgets between adults of a pair.

Ospreys in Antigonish County, Nova Scotia, use two different habitats: nesting within 3.5 km of estuaries and capturing winter flounder (*Pseudopleuronectes americanus*) in the estuaries; and nesting inland, usually beside lakes and/or streams and feeding primarily on white sucker (*Catostomus commersonei*), alewife (*Alosa pseudoharengus*), and blueback herring (*A. aestivalis*). Prévost (M.Sc. thesis, MacDonald College, McGill Univ., Montreal, Quebec, 1977) suggested that inland nesters feed on the latter two species in that portion of the nestling period coinciding with the spawning migration of these fish. He also noted these birds might have to shift foraging locations from lakes and/or streams to estuaries in years that the herring migration ceases before their young fledge.

In our study we attempt to identify major breeding activities of inland and coastal nesting pairs and to determine the extent of changes in relative time devoted to hunting by males throughout stages of the breeding cycle.

Use of the two anadromous herring species by inland nesters and the possible significance of a shift in foraging locations during the nestling period are assessed. Also, we have hypothesized that the length of time of hunting by coastal birds would be less variable than that of inland birds since flounders in the two estuaries used by the study population are available to Ospreys throughout the breeding season (Prévost 1977).

Study site and methods.—This study was conducted within the watersheds of Antigonish and Pomquet estuaries in northeastern Nova Scotia (Fig. 1). The West and South rivers are the two major watershed systems emptying into Antigonish Estuary and water from shallow, eutrophic Gaspereaux Lake meets the West River about 11 km from Antigonish estuary.

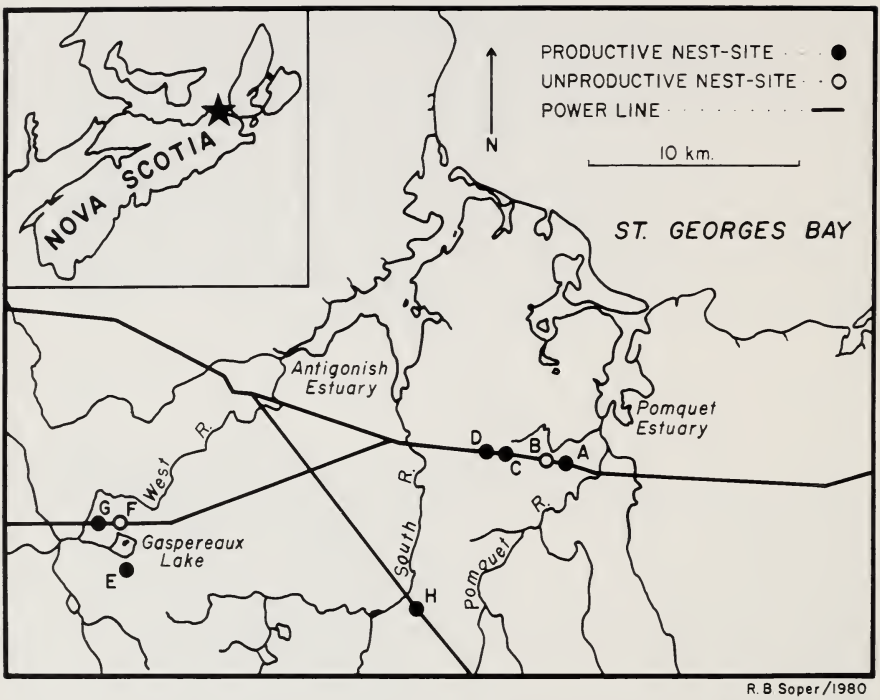


FIG. 1. Locations of Osprey nest-sites studied in Antigonish County, Nova Scotia, in 1978. The star in the insert shows the location of the study area in Nova Scotia.

Ospreys fished almost exclusively in these two estuaries, the two rivers, and Gaspereaux Lake.

Most Ospreys that fished primarily in the estuaries nested on Nova Scotia Power Corporation power poles about 3 km south of and approximately midway between the two estuary systems (Fig. 1). Adults at four nests, 0.25–1.2 km apart, were intensively observed.

Inland nest-sites were no closer to each other than 0.25 km and both trees and power line poles were used as nest-sites. Two intensively observed nests were on power line poles between Gaspereaux Lake and the West River, approximately 10.8 km from Antigonish estuary, 0.8 km from Gaspereaux Lake, and 0.5 km from the West River. A third inland nest was located in a live white spruce (*Picea glauca*) 0.6 km from Gaspereaux Lake, and 12 km from Antigonish estuary. A fourth inland nest was situated on a hilltop power pole 2.4 km from the South River and 9.0 km from Antigonish estuary (Fig. 1).

The timing and duration of spawning migration of the two herring species are variable but both species usually begin by mid-May and end early in July. The alewives are in the river from approximately 15 May until 15 June and the blueback herring from 15 June until 15 July, although there are few fish left after mid-July. Blueback herring spawn in rivers and lakes but alewives usually spawn in lakes.

Nests were initially located and periodically surveyed by helicopter. Elevated blinds were erected within 100–300 m of each nest, allowing unobstructed surveillance of nests and nearby trees in which birds perched. Breeding activities from egg-laying through fledging were

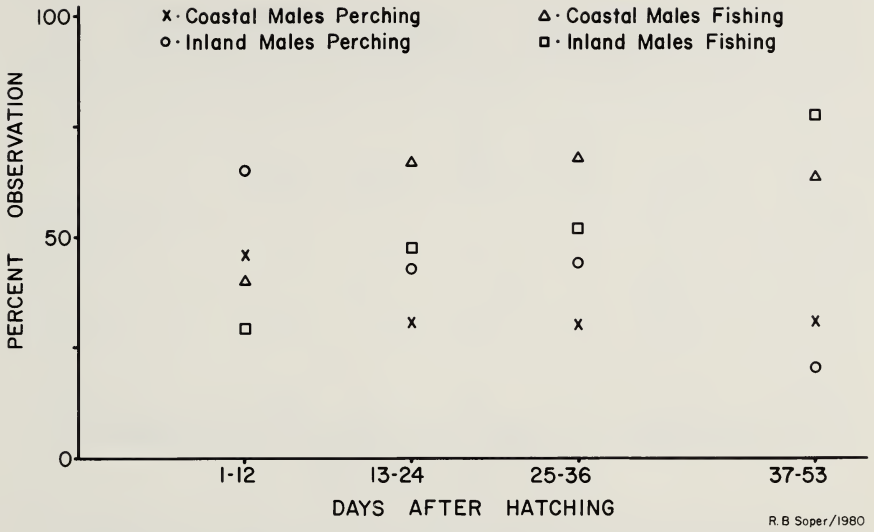


FIG. 2. Percentage of time spent by inland and coastal males fishing and perching near nests during the nestling period.

observed at nest-sites from 9 May–22 August 1978, for a total of 487 h. Daily observations were made from 06:00–11:00, 11:00–16:00, and 16:00–21:00. One day the observation period included the 06:00–11:00 and 16:00–21:00 periods, and the next day the 11:00–16:00 period. A different nest was watched during each observation period and each nest was usually observed at least once every 4 days.

Initially, three inland nests were watched. However, one nest was destroyed by wind early in the season and, to retain sample size, we shifted observations to another nest on the South River watershed. Three coastal pairs were also studied but young from one nest (site B) disappeared and we shifted observations to another nest (site A).

Initially sex of the birds was determined by their relative positions during copulation. Later it was noted that each female of the eight pairs watched had a darker breast patch than her mate. Similar results were found by MacNamara (U.S. Natl. Parks Serv. Trans. Proc. Series 2:43–45, 1977), although he looked at males and females in general and not pairs.

We subdivided the breeding season as follows: (1) pre-incubation (before egg-laying), (2) incubation (from the onset of egg-laying to hatching of the first egg), and (3) nestling (from the first appearance of young until the first young fledged). Pre-incubation was relatively short and data were collected from only three nests. Fishing time spanned the period from departure from the nest-site until a bird returned with a fish. Although we could not be sure that males hunted during this entire period, males usually fish continuously while in these two estuaries (Seymour, unpubl.), and in this study, always returned to their nests from the direction of the estuaries. Since males sometimes ate part of fish before returning to their nests (see also Prévost 1977), fishing duration included the time males spent eating. However, eating time for females was precisely recorded and encompassed the time females spent feeding themselves and their young.

Identification of fish species was relatively easy because they differ markedly in form and

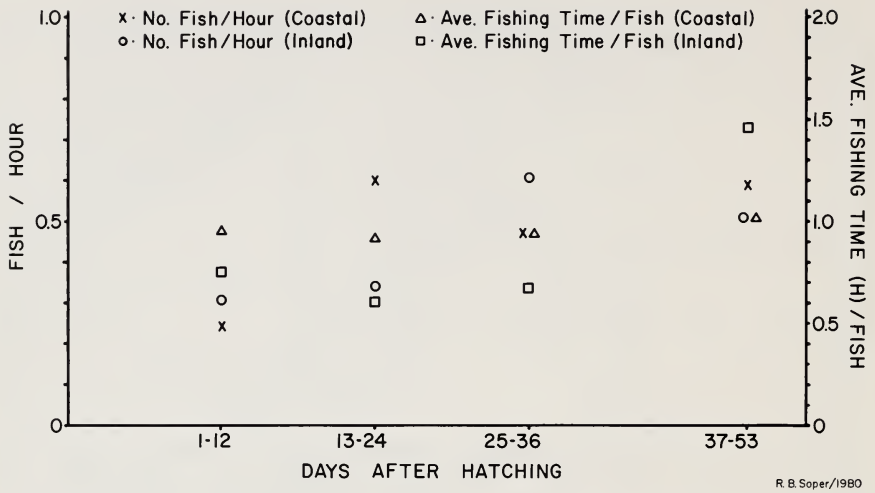


FIG. 3. Average duration of fishing and number of fish brought back to nests (per hour of observation) by inland and coastal nesting male Ospreys during the nestling period.

color. However, size of fish was so difficult to estimate accurately that we did not attempt to do so. A concurrent study of the chronology of the migration of the two herring species in the West and South rivers allowed us to determine the relationship between shifts in foraging locations of Ospreys and changes in the distribution or abundance of these fish.

Time budget analysis.—During pre-incubation females mostly sat beside or on the rim of their nests. Males gathered nesting materials, nest-built or perched near nests. Females rarely fished and males averaged only one hunt per 5-h observation period with a mean yield of 0.18 fish/h (five fish in 28.2 h).

Eggs were rarely left unattended during the incubation period. Bent (U.S. Natl. Mus. Bull. 167, 1937) and Ames (J. Appl. Ecol. Suppl. 3:87–97, 1966) said that only females incubated eggs. However, females in the present study incubated during approximately 66% of the daylight hours and males incubated the rest of the time. Similar results for males were reported by Garber and Koplin (Condor 74:201–202, 1972) and Levenson (1976). Green (1976) reported that female Ospreys incubated during the night and this appeared to be the case in our study. When not incubating, females usually perched within 200–300 m of the nest. Females never hunted during the incubation period and duration of fishing bouts by males and their yields of 0.18 fish/h (38 fish in 215 h) did not differ from bouts and yields of the pre-incubation period.

Only females brooded and fed nestlings. Intensive brooding lasted only until nestlings were 5–6 weeks old. Females continued to feed the young until they were approximately 7–8 weeks old. Nestlings of this age fed without assistance from females on only 5 of the 115 fish we saw them consume; they ate all of thse fish entirely by themselves.

Male fishing time increased dramatically, becoming the dominant activity during the nestling period. Accordingly, yields increased 2.5 times to 0.44 fish/h (108 fish in 243.5 h). Females began fishing when nestlings older than 7–8 weeks started feeding themselves, although they only contributed 7 of 115 fish brought back to nests.

Differences in activities of coastal and inland nesters.—There was no significant difference between inland and coastal males in the percentage of daylight hours spent fishing during

Table 1

Comparison of Time Spent at Major Activities by Coastal and Inland Nesting Osprey Pairs Before and After Inland Birds Shifted Foraging Locations

	Duration of observation (h)	Male fishing (%)	Male perching near nest (%)	Female feeding young (%)	Fish consumed/h	Fishing time (h) $\bar{x} \pm SD$
Inland nesters						
Before shift	83.5	35.4	56.7	9.8	0.42 (N = 35)	0.6 ± 0.4 (N = 31)
After shift	55.2	74.0	23.6	11.5	0.53 (N = 29)	1.4 ± 0.6 (N = 21)
Coastal nesters	104.8	60.3	35.2	12.0	0.49 (N = 64)	1.0 ± 0.5 (N = 40)

the incubation ($\chi^2 = 1.15$, df = 1, $P > 0.25$) and nestling ($\chi^2 = 2.04$, df = 1, $P > 0.10$) periods. Similarly, there was no difference in female eating time for the two periods ($\chi^2 = 0.04$, 0.15; df = 1; $P > 0.90$, 0.50). Since females fed their young in one continuous bout as soon as their mates deposited fish at their nests, female eating time reflects the amount of fish provided by males.

The percentage of time spent fishing by coastal males remained relatively stable throughout the breeding period (Fig. 2). However the duration of fishing by inland nesters increased markedly during the nestling period, at the expense of time spent near nest-site. The increase in the duration of fishing resulted from a shift in foraging locations, from inland lakes and streams to estuaries. Inland birds travelled an average of 23.0 km to forage after the shift, compared to 2.3 km before the shift.

The shift in foraging sites reflected a change in prey availability. Inland nesters presumably nest near lakes and/or streams to take advantage of the spawning migration of anadromous alewives and blueback herrings. The alewife run occurred between 15 May and 7 June (Dill, unpubl.). Thus this run predates the Osprey nestling period when the demand for food was greatest. However, alewives traditionally spawn in Gaspereaux Lake which is connected to the West River. In some years, some fish were stranded in the lake by lowered water levels and available to Ospreys after the migratory run in the streams was over. The blueback herring migration is traditionally later in the season than that of the alewife and Dill (unpubl.) reported this herring in the West River between 13 June and 15 July 1978. The blueback spawned in rivers and lakes and were available to Ospreys until approximately mid-way through the nestling period. Consequently, blueback herring were the main prey of most inland nesters during the nestling period. When numbers of this fish dwindled, male Ospreys were seemingly forced to shift to estuaries to fish for flounders. Once the shift to flounders occurred, herring were no longer brought to nests. Birds followed rivers on their way to estuaries and still caught suckers after the shift, although the availability of these fish decreased toward the end of the spawning season when they moved to deeper water.

Figure 3 shows that mean foraging time was constant for coastal males throughout the nestling period. Inland males spent less time fishing than coastal males early in the nestling period but fishing time increased substantially for them later. However, the number of fish brought to nests did not reflect duration of fishing. The three inland pairs on which the results are

Table 2

Average Time Required for Females to Feed Different Species of Fish to Their Young[a]

Fish species	N	Time (h) $\bar{x} \pm$ SD (range)
Winter flounder	26	0.2 ± 0.1 (0.1–0.4)
Alewife/blueback herring	10	0.2 ± 0.1 (0.1–0.4)
White sucker	6	0.4 ± 0.2 (0.2–0.7)
White perch (*Morone americana*) and/or yellow perch	3	0.2 ± 0.1 (0.1–0.3)

[a] Refers to only whole fish that were consumed immediately, in one continuous bout.

based did not shift to estuaries to forage at the same time, and much of the period (25–36 days, 64% of observation time) included observation of birds that had not made the shift. There was a significant difference ($t = 7.5$, df = 41, $P < 0.005$) in the mean time required for Ospreys to catch herring and suckers in streams and flounders in estuaries.

To show the full impact of the shift to different foraging sites on the mean foraging time, data were analyzed on a before- and after-shift basis (Table 1). Fishing time for the three inland birds increased by 109% (perching time decreased 140%) after the shift; there was a significant ($t = 6.07$, df = 50, $P < 0.005$) increase in the mean duration of hunts/fish. Inland males fished significantly less than coastal males before ($t = 4.58$, df = 69, $P < 0.0025$) the shift. Despite differences in fishing time, inland and coastal males brought the same number of fish to their nests; inland males returned 0.46 fish/h (64 fish in 138.7 h of observation) and coastal males 0.49 fish/h (51 fish in 104.8 h).

Coastal males mainly caught flounders (39 of 40 identified fish) but inland males caught two yellow perch (*Perca flavescens*), 12 suckers, 16 herring, and 17 flounders. Although brought to nests less often than herring and flounders, suckers were larger than any other species and it took females twice as long to feed this fish to young as it did to feed them flounders ($t = 5.73$, df = 30, $P < 0.0025$) (Table 2). Suckers were usually partly consumed by males (8 of 12 fish) before being brought to nests, but flounders were almost always (45 of 51 fish) brought whole. Since there was no significant difference in time spent feeding their young by inland and coastal females, it appears that during the nestling period both inland and coastal males provided their mates and young with approximately the same amount of fish tissue.

Inland males shifted fishing sites at different times; males at sites H, G, and E shifted on approximately 12 July, 21 July, and 7 August, 25, 34, and 45 days, respectively, after their first chick hatched. This variability in time of shifting fishing sites may have resulted, in part, from differences in the timing of the herring runs in the West and South rivers (Prévost, unpubl.). However, the availability of stranded alewives in Gaspereaux Lake to males at sites G and E after the main run probably influenced timing of the shift of fishing sites. The site H male did not fish in Gaspereaux Lake. Although the male from site F continued to catch herring in the above lake, the male from site G stopped fishing there 17 days before the site E male shifted to the estuary. In general, Ospreys infrequently fished in Gaspereaux Lake and the rivers after mid-July, suggesting that fish were either unavailable or perhaps too few in number to make fishing worthwhile.

The average fishing time after the shift for males E and G increased 243% and 140%, respectively, and both caught mostly (>75%) flounders after the shift (Table 3). The average hunting time for male H increased only 56% as flounders represented less than half the fish

TABLE 3

PERCENTAGE OF TIME DURING THE NESTLING PERIOD FOR MALE FISHING AND FEMALE FEEDING, BEFORE AND AFTER A SHIFT IN FISHING AREAS BY THREE INLAND NESTING PAIRS

	Site E	Site G	Site H
Before shift	35[a]	34[a]	14.5[a]
Male fishing	24.1%	46.1%	37.4%
Mean duration of fishing bouts (h)	0.4 ± 0.3 (N = 16)	0.8 ± 0.5 (N = 11)	0.8 ± 0.1 (N = 4)
Percent flounders brought to nest	0	0	0
After shift	14.2[a]	12.4[a]	28.5[a]
Male fishing	66.7%	87.9%	71.6%
Mean duration fishing bouts (h)	1.4 ± 0.3 (N = 9)	1.9 ± 0.3 (N = 4)	1.2 ± 0.7 (N = 15)
Percent flounders brought to nest	77.8 (N = 9)	75.0 (N = 4)	46.7 (N = 15)

[a] Hours of observation.

brought to the nest. Although this male shifted to flounders earlier than the other males, he continued to catch suckers after the shift.

Conclusions.—Flounders, although smaller and lower in calorific value than herring or suckers (Prévost, 1977), were a permanent, if patchily distributed, resource. Use of flounders means that coastal Ospreys need not shift to a new foraging site during the nestling period. Inland nesters could experience a depletion or lack of herring and suckers prior to fledging of their young. Adult male Ospreys could then shift to foraging for flounders in estuaries. In 1978, inland male Ospreys brought as many fish to their nests after the shift as before. Although not a problem in 1978 the year of our study in this habitat, where climatic factors are variable a change in conditions could influence the availability of herring and make it difficult for inland male Ospreys to provide their nestlings with adequate fish.

Nest-site location relative to the foraging site likely influences the amount of time a male can spend at the nest-site. A male Osprey frequently interacts with other Ospreys, as well as other species, perhaps protecting the nest from intruders (Jamieson, unpubl.).

Both coastal and inland habitats have been used for nesting since at least 1974 when surveys of this population were begun. There has been variation from year to year both in the number of birds using each habitat and in the relative reproductive success of pairs. However, use of both nesting habitats appears well established. Birds were on nest-sites within a few days after arrival on the study area and hostile interactions between pairs were rare when nest-sites were being established; this suggests that birds were not forced by competition to use sub-optimal habitat. Furthermore, comparison of fledging success (cf. Postupalsky, Raptor Res. Rept. 2:21–31, 1974) shows no significant difference ($t = 1.11$, $df = 20$, $P > 0.20$) between the coastal and inland nesters; five inland pairs produced 1.8 young per pair and 17 coastal pairs produced 1.2 young per pair. Choice of habitat presumably reflects the ability of a male to provide himself, his mate, and their young with food while maximizing the amount of time spent near the nest.

Acknowledgments.—Aspects of this study were supported by St. Francis Xavier University (University Council for Research) and the Natural Sciences and Engineering Research Council of Canada (operating grant No. A6217 to Seymour). The Nova Scotia Department of Lands and Forests assisted by providing manpower, transportation, and aircraft time. The Atlantic Provinces Inter-University Committee on the Sciences provided Jamieson with a Student Summer Research Assistantship. Dave Longard, Dan McKenna, and Murray Workman assisted with fieldwork. P. C. Smith of Acadia University and F. C. Zwickel of the University of Alberta provided comments and suggestions in writing the manuscript.—Ian Jamieson, *Dept. Biology, Acadia Univ., Wolfville, Nova Scotia, Canada*; Norman R. Seymour, *Dept. Biology, St. Francis Xavier Univ., Antigonish, Nova Scotia B2T 1C0, Canada*; and Robert P. Bancroft, *Nova Scotia Dept. Lands and Forests, Antigonish, Nova Scotia B2G 1R6, Canada.* *Accepted 15 Feb. 1982.*

Wilson Bull., 94(4), 1982, pp. 564–565

Nest provisioning behavior by a male Northern Harrier on the death of his mate.—At about 10:00 on 16 May 1980, at Malheur National Wildlife Refuge, Harney Co., Oregon, Thompson observed an adult female Northern Harrier (*Circus cyaneus*) carry a small mammal to a nest. The nest, which was located in a broad-fruited burreed (*Sparganium eurycarpum*) over 30 cm of water, contained three young and a pipping egg. The young were estimated to be under 10 days old, based on comparisons to other nestlings of known age.

When we reexamined the nest on 3 June, it contained one live, 3-week-old nestling and one dead nestling of about the same age. A dead adult female harrier was found floating ventral side down 0.5 m from the nest. The nest was littered with prey carcasses. Of 36 whole prey counted on and around the nest, most were montane voles (*Microtus montanus*) or long-tailed voles (*M. longicaudus*), but a few ground squirrels (*Spermophilus* sp.) were present. Some prey were fresh, while others were in various stages of decay. Of 10 harrier nests examined from incubation to fledging in 1980, only this one contained prey remains. Watson (The Hen Harrier, T. and A. D. Poyser, Ltd., Berkhamsted, Hertfordshire, England, 1977) reported that the female harrier removes uneaten food from the nest until the chicks can feed themselves. Beske (pers. comm.) also found this to be true with his research on harriers in Wisconsin.

The nest was visited again on 12 June. The surviving nestling appeared healthy and about to fledge. Heysham (1783, cited *in* Watson 1977) reported seeing a male harrier feeding chicks and further stated that a male could rear a brood after his mate was killed. Watson (1977) could find no recent reports of male harriers feeding chicks. He stated that the nestlings would likely survive only if they were well developed and capable of tearing up prey for themselves.

We do not know if the adult male was feeding the surviving nestling or simply bringing prey to the nest. Breckenridge (Condor 37:268–276, 1935) reported that a male's visits to a nest lasted only long enough to release prey. Watson (1977) observed a male visit a nest repeatedly and remain there for a minute or more, but did not see the male feed nestlings. In our case, the nestling appeared large enough and strong enough to feed itself. After the death of a female harrier in Wisconsin, Beske (pers. comm.) recorded a similar nest history in which a male continued to provide prey to a nest containing nestlings.

The dead female was clearly visible from above. We did not remove her from the vicinity of the nest, because of the possibility that her presence may have stimulated the male to continue provisioning the nest. To the best of our knowledge, this is only the third record

of a male Northern Harrier continuing to bring prey to a nestling following the death of his mate.—Steven P. Thompson and John E. Cornely, *U.S. Fish and Wildlife Service, Malheur National Wildlife Refuge, P.O. Box 113, Burns, Oregon 97720.* *Accepted 1 Mar. 1982.*

Wilson Bull., 94(4), 1982, pp. 565–566

Notes on the hunting behavior and diet of the Crested Caracara in northeastern Chiapas and Tabasco, Mexico.—Crested Caracaras (*Polyborus plancus*) are opportunistic scavengers that forage on the ground, feed on carrion, and pirate prey (Bent, U.S. Natl. Mus. Bull. 170, 1938; Sprunt, North American Birds of Prey, Maaper and Bros., New York, New York, 1955; Glazener, Condor 66:162–163, 1964). Caracaras seldom have been observed chasing birds and we know of only two recorded incidents of caracaras catching adult birds. Bent (1938) reported that a caracara chased and killed a White Ibis (*Eudocimus albus*), and Brown and Amadon (Eagles, Hawks and Falcons of the World, McGraw-Hill, New York, New York, 1968) note that three or four caracaras pursued and captured an egret.

During March and April, 1977 and 1978, we observed caracaras in the area between Villahermosa, Tabasco, and Palenque, Chiapas. The region is level coastal plain 50–200 m elev., and is characterized by extensive cattle pasture dotted with trees, snags, and groves of remnant tropical moist forest.

Here, we describe four caracara hunts, three directed at Cattle Egrets (*Bubulcus ibis*) and one at a Brown Jay (*Cyanocorax morio*). Three hunts were made by duos of caracaras and one was made by a lone caracara.

On 13 April 1977 at 09:13 we watched a caracara fly into a flock of 10–15 Cattle Egrets which were flying at approx. 30 m. Very soon an egret separated from the flock and the caracara pursued it. At this point another caracara headed toward the first and joined the pursuit. Quickly a pattern became evident. The egret turned evasively to one side every time a caracara approached to within 1 m. As the caracaras' turning ability was poorer than that of the egret, the pursuing raptor continued off at a tangent each time the egret turned. At each turn, the other caracara continued the pursuit. After about 2 min, the egret dropped down, passed through a grove and among some tall shrubs, and then began climbing. The caracaras continued the pursuit until the egret had flown to 60–90 m altitude when the raptors soared away together. This encounter lasted about 2–3 min.

The second egret hunt occurred at 08:15 on 21 March 1978. A lone caracara flushed a flock of 50–100 Cattle Egrets from a pasture a few hundred meters in front of it. The caracara flew toward the flock, following as it turned in a wide arc. The egrets climbed and turned back and forth in close ranks. At this point a second caracara began following the first. Based on its smaller size, the first caracara could have been a male. When the egrets were about 60 m above the ground, the male broke off the chase, while the female was about 120 m distant, chasing a lone egret also at 60 m, the male joining her pursuit. After a few seconds, the egret dove straight down, and the female stooped, gaining rapidly on the egret. All three birds disappeared behind vegetation until both caracaras flew up from the area 3 min later. Evidently the egret had escaped. The time elapsed until the stoop was about 3 or 4 min.

The third incident involving a single caracara and Cattle Egret occurred on 17 April 1978. At 17:35 an adult caracara flew into view, pursuing a Cattle Egret. As in the hunts already described, the encounter was characterized by tight, twisting, evasive flight by the egret with the raptor gaining on the egret in straight flight and falling behind in the turns. The caracara seemed to seek a height advantage over the egret during the 2 min of observation, but did not succeed before the pursuit continued out of sight.

The fourth hunt was observed at 11:00 on 18 March 1978. A Brown Jay, pursued by two carcaras which were alternately making passes at it, flew over a road in level flight at less than 20 m. The jay dove into a 5 m tree and was followed by one of the caracaras, which hopped from limb to limb while the other flew around the tree. The jay then flew from the tree, pursued by both caracaras, and perched in another small tree 100 m away. At least one of the raptors perched in this tree, looking down into it for 20 sec before flying off, followed by the other caracara. The duration of this encounter was about 2 or 3 min.

Although we did not see caracaras catch Cattle Egrets or other large birds during these four hunts, we believe they sometimes succeed. We found evidence that caracaras at one nest had been feeding heavily on Cattle Egrets. On 21 March 1978 we found remains of four Cattle Egrets lying below and hanging in a palm occupied by one of two fledgling caracaras which were raised at this nest-site about 1 km from the site of one or our hunting observations. A Cattle Egret had been plucked by a raptor on the ground nearby. That only one of 12 Cattle Egret long bones, and none of the slender leg bones, was broken, may be taken as evidence that the egrets were not collected as highway carrion. Other remains present included those of a lizard (*Ctenosaur* sp.) and a second lizard of the same or similar species. Of eight pellets found, seven contained white feathers and one those of an Indigo Bunting (*Passerina cyanea*), three contained fur, and five contained lizard scales. One contained a vertebral spine of an iguanid, one contained a small rodent jaw, and one a piece of a grasshopper (Orthoptera) leg. Indigo Buntings and the large lizards are frequently road-killed in the region. On two of five occasions we noted caracaras feeding on road-kills, comprising a *Ctenosaur* sp. and an *Iguana* sp.

This note is Contribution No. 91 of the Chihuahuan Desert Research Institute, Alpine, Texas. Hal Flanders and Jeff Wehmeyer took part in these observations, and Peter Lawson reviewed the manuscript. Fieldwork yielding these observations was supported by the Frank Chapman Memorial Fund, the World Wildlife Fund, and the Chihuahuan Desert Research Institute.—David Whitacre, Devora Ukrain, and Gary Falxa, *Chihuahuan Desert Research Institute, Box 1334, Alpine, Texas 79830.* (Present address DW: *P.O. Box 456, Coloma, California 95613.*) *Accepted 15 Jan. 1982.*

Wilson Bull., 94(4), 1982, pp. 566–567

Florida Red-shouldered Hawk robs American Crows.—The following interactions were noted while my wife and I were following the breeding behavior of Florida Red-shouldered Hawks (*Buteo lineatus alleni*) and a pair of American Crows (*Corvus brachyrhynchos*) in January and February 1981, at the Hendrie Ranch, 24 km S of Lake Placid, Highlands Co., Florida. Both species foraged near a water hole where walking catfish (*Clarias batrachus*) were concentrated due to a drought. River otter (*Lutra canadensis*) fed on the fish over a 3-week period and crows scavenged fish heads left by the otter. On 19 January six to eight crows had retrieved seven fish heads from the water edge and were removing an eighth, when a Red-shouldered Hawk landed among them. The crows moved 15–30 cm away. The hawk seized the catfish and flew off to a tree. Four days later an otter, attended by two crows, had finished eating and was walking up the bank when a red-shoulder landed almost on top of it. There was no fish head and the hawk flew off. On a following morning I watched a crow retrieve two heads from the water and struggle to hold both in its bill. A red-shoulder swooped on the crow which dropped both heads, one of which was seized by the hawk.

The crows sometimes cached fish heads in clumps of grass in the nearby pasture. A crow, attended by two others, had pulled a catfish head from the grass when a red-shoulder alighted within 15 cm. This time its back was to me, wings slightly out, and tail spread over the

grass, looking from side-to-side as five crows quickly joined the first three. Two crows briefly assumed agonistic postures with bills lowered and feathers of head and neck raised. After a few moments, the crows started to leave and the hawk flew off with the fish head.

While walking near the water hole on 2 February I saw a crow flying toward its nest, then being built, with a black lump in its bill, pursued by a Red-shouldered Hawk. Ten min later I noted two crows pulling up pieces of sod which they wadded in their bills. They had just left to fly back to the nest when the hawk attacked as before and pursued them over the water. Within 15 min one of the crows took a piece of sod, larger than the others, to the branch of a tree. Here, with the sod held in its feet, it delivered blows with its bill. The hawk swooped a third time, nearly hitting the crow and again with no effect. Although Florida Red-shouldered Hawks use "clumps of grass roots" in their nests (Nicolson, Wilson Bull. 42:32–35, 1930), the hawks I watched did not start to build their nest until 2.5 weeks later. I wondered if the hawk, on seeing the crows handle the sods, thought that they had some kind of prey.

I have encountered no previous accounts of Red-shouldered Hawks robbing or attempting to rob American Crows. Brockman and Barnard (Anim. Behav. 27:487–514, 1979), in their review of kleptoparasitism, give no mention of *B. lineatus* in a list that includes many raptors.—LAWRENCE KILHAM, *Dept. Microbiology, Dartmouth Medical School, Hanover, New Hampshire 03755.* *Accepted 15 Mar. 1982.*

Wilson Bull., 94(4), 1982, pp. 567–569

Feeding behaviors and efficiencies of Common and Forster's terns.—Aerial feeding, either by plunge-diving or hover feeding, has been described for Common Terns (*Sterna hirundo*) (LeCroy, Wilson Bull. 84:201–202, 1972; Dunn, Nature 244:520–521, 1973; Erwin, Ecology 58:389–397, 1977), Sandwich Terns (*S. sandvicensis*) (Dunn 1973; Rodgers, Wilson Bull. 87:420, 1975), Royal Terns (*S. maximus*) (Rodgers 1975, Erwin 1977), Forster's Terns (*S. forsteri*) (Salt and Willard, Ecology 52:989–998, 1971; Rodgers 1975), and Crested Terns (*S. bergii*) (Feare, Condor 77:368–370, 1975). Herein we describe a previously unreported feeding strategy for Forster's Terns, and compare its efficiency to that of aerial feeding by both Forster's and Common terns.

Data were collected from 4–23 August 1980 and involved 6 h 34 min of actual observation time. Study sites were northern and southern beaches of Wallops Island, Accomack Co., Virginia and a bridge over a causeway leading from the mainland to Chincoteague Island, Virginia, (Accomack County; 75.5°W, 38°N). The first two sites hosted only Common Terns, while the third was used almost exclusively by Forster's Terns.

We made 81 and 82 individual observations of Common and Forster's terns, respectively, predominately between 06:00 and 11:00. We recorded species of each bird, total number of dives, number of successful dives, number of foraging dives while in flight, and use of a technique previously unreported for Forster's Terns—diving for food directly from a perch on the bridge, approx. 5 m above the surface of the water. In this latter technique a tern stood on the edge of the railing with head lowered to the level of its feet, and tail extending directly along the longitudinal axis of the body. Searching was done by turning the head from side to side, scanning, with the bill oriented downward. When a prey item was spotted, the tern opened its wings slightly, then quickly closed them, and then dropped from its perch to the water. During the dive, the wings unfolded enough to facilitate slight changes in course. Up to six individuals simultaneously fed in this manner.

At the bridge site Forster's Terns were feeding both aerially and from perches. The aerial feeders were feeding within 3 m of the bridge, presumably taking the same prey resources

Table 1

Comparison of Numbers of Attempts and Successes per min for Prey by Common and Forster's Terns

	df	Attempts/min		Successes/min	
		$\bar{x}$	t_{calc}	$\bar{x}$	t_{calc}
Common Terns	158	1.955	3.350**	0.648	0.207
Forster's Terns		1.373		0.666	
Common Terns	109	1.955	3.206*	0.648	2.626*
Forster's Terns (aerial-feeders)		1.323		0.429	
Forster's Terns (perchers)	78	1.399	0.621	0.810	4.595**
Forster's Terns (aerial-feeders)		1.323		0.429	

* $P \leq 0.01$, ** $P \leq 0.001$.

as were the perching feeders. The area in which the Common Terns fed lacked perches. Feeding efficiencies (successful dives/attempts) were compared using contingency χ^2 tests: (1) between species, (2) between perched and non-perched Forster's Terns, and (3) between Common Terns and aerially feeding Forster's Terns. Using the Student's *t*-test, the above groups were tested for differences in numbers of attempts and successes per minute.

Forster's Terns (46% efficiency) fed more efficiently than Common Terns (32% efficiency) ($\chi^2 = 10.11$, df = 1, $P \leq 0.005$). Among Forster's Terns alone, aerial feeders had a 37% feeding efficiency, whereas perching individuals had a 51% efficiency ($\chi^2 = 12.41$, df = 1, $P \leq 0.005$). No significant difference in efficiency was found between aerially feeding Forster's and Common terns ($\chi^2 = 0.09$, df = 1, $P > 0.05$).

Common Terns made more attempts/min for food than did the Forster's Terns ($P \leq 0.001$), but they were no more successful ($P \geq 0.05$) (Table 1). Compared to Common Terns, aerially-feeding Forster's Terns made more attempts for food/min and were more successful ($P \leq 0.01$). No difference in the number of attempts/min was found between the aerial and perching Forster's Terns ($P \geq 0.05$); however, the perch strategists had more success/min ($P \leq 0.001$). Perch-feeding terns, therefore, expended less energy searching for food than did aerial feeders, and procured more food per unit of time.

Salt and Willard (1971) recorded 22–29% capture efficiency by Forster's Terns during the summer, which is lower than the efficiency of our aerial feeders and considerably lower than that of our perched feeders. Efficiencies of Common Terns reported by Dunn (1973) ranged from 17–39%, overlapping our observed efficiencies. Rates of success Dunn (1973) measured were comparable (0.23–0.5 captures/min) to those we recorded (0.34 captures/min). Erwin (1977) recorded rates approximately one-half of our rates. Although the reason(s) for this difference is unknown, perhaps prey density influences rates of capture.

Forster's Terns apparently possess the behavioral plasticity to use man-made perches. Because capture efficiency was greater and energy expenditure less when foraging from perches than when flying, we expect that Forster's Terns compete for suitable perches. Such competition may have important long-term consequences for terns in coastal areas where man-made perches are available.

We would like to thank J. Barlow, G. Fox, S. Ha, D. McCracken, and L. Oring for contributions to the manuscript. This study was paid for by a grant from the Millersville State College Alumni Association.—J. Michael Reed, *Dept. Biology, Millersville State*

College, Millersville, Pennsylvania 17551, HERBERT E. HAYS, *Dept. Biology, Shippensburg State College, Shippensburg, Pennsylvania 17257,* AND DAVID A. ZEGERS, *Dept. Biology, Millersville State College, Millersville, Pennsylvania 17551.* (Present address JMR: *Dept. Zoology, Univ. Montana, Missoula, Montana 59812.*) *Accepted 20 Jan. 1982.*

Wilson Bull., 94(4), 1982, pp. 569–571

Clutch-size and prefledging survival in Red-winged Blackbirds at Williamstown Lake, New Brunswick.—Studies of clutch-size and survival of the Red-winged Blackbird (*Agelaius phoeniceus*) were summarized by Francis (Wilson Bull. 83:178–185, 1971; Auk 92: 815–817, 1975), Dolbeer (Auk 93:343–355, 1976), and Brown and Goertz (Wilson Bull. 90: 261–270, 1978). The Maritime Provinces of Canada represent the northeastern range limit of the species, and of its preferred habitat, cattail (*Typha latifolia*) marshes. I documented clutch-size and prefledging survival of red-wings for a dystrophic lake in New Brunswick. This lake has an intermixture of vegetation characteristic of the red-wing's preferred temperate zone cattail habitat and also ericaceous vegetation, more typical of the boreal zone. My clutch-size data were also compared to the Maritime Nest Records Scheme (MNRS) data compiled from cattail marsh and upland habitat.

Study area and methods.—Williamstown Lake, New Brunswick (46°20′N, 67°40′W) is a shallow (<7 m) man-made dystrophic lake of 370 ha adjacent to mixed forest and farmland. Nesting habitat included cattail, leatherleaf (*Chamaedaphne calyculata*), rhodora (*Rhododendron canadense*), bog rosemary (*Andromeda glaucophylla*), Labrador tea (*Ledum groenlandicum*), sedges (*Carex* spp.), and locally, wild rice (*Zizania aquatica*), all growing through a floating *Sphagnum* mat. Nests were generally found attached to dead cattail stalks and/or stems of one of the ericaceous species.

I started observing on 22 May 1976 while males were still courting females. Nests were revisited every three days to record clutch- or brood-size. Clutch-size was determined for 25 nests at Williamstown Lake and was summarized from 155 cards in the MNRS. Nest record usage was restricted to cards with a minimum of two-clutch entries, equal in size and from different days, to ensure that laying had ended.

Definitions of prefledging mortality follow Caccamise (Condor 80:290–294, 1978). Prefledging survival was calculated for 37 active nests using nest success, fledging success, and daily survival probability values.

Results and discussion.—I found only clutches of three and four eggs at Williamstown Lake (Table 1) compared to a clutch range of 2–7 eggs from the MNRS. The mean clutch-size (3.4 ± 0.5) at Williamstown Lake was significantly lower than the mean for the MNRS data for the Maritimes as a region ($\bar{x}$ = 3.7 ± 0.7, Mann-Whitney *U*-test, *U* for large samples = 1.67, $P < 0.10$), for New Brunswick ($\bar{x}$ = 3.7 ± 0.7, *U* for large samples = 1.78, $P < 0.10$), and for Nova Scotia ($\bar{x}$ = 3.7 ± 0.9, *U* for large samples = 11.52, $P < 0.001$), but did not differ significantly from the mean (3.6 ± 0.9) for the MNRS data for Prince Edward Island (*U* for large samples = 0.18, $P > 0.20$). The small mean clutch-size I found at Williamstown Lake is a consequence of the larger ratio of 3-:4-egg clutches found at Williamstown Lake (Table 1) and may suggest poorer quality nesting habitat. A larger sample for Williamstown Lake would have enabled a better comparison.

Predation accounted for the greatest loss of eggs or nestlings (Table 2) at Williamstown Lake, as has generally been found for other areas. Two nests (six eggs) were deserted following discovery for which I may have been responsible. However, evidence was inconclusive since incubation continued in similarly visited nests nearby.

Table 1

Clutch-size of Red-winged Blackbirds at Williamstown Lake, New Brunswick, and from Records of the Maritime Nest Records Scheme

Location	N	2	3	4	5	6	7	$\bar{x}$	±SD	Ratio of 3-egg : 4-egg clutches
Williamstown Lake	25	0	14	11	0	0	0	3.4	0.5	1.27
New Brunswick[a]	56	2	17	35	1	0	1	3.7	0.7	0.48
Nova Scotia	26	1	6	18	1	0	0	3.7	0.9	0.33
Prince Edward Island	73	2	31	35	5	0	0	3.6	0.7	0.88
MNRS total	155	5	54	88	7	0	1	3.7	0.7	0.60
Total	180	5	68	99	7	0	1	3.6	0.7	0.68

[a] Not including data from Williamstown Lake.

Different indices of prefledging survival (e.g., nest success and fledging success) have given different estimates of success for previous studies (Smith, Ecology 24:183–207, 1943; Goddard and Board, Wilson Bull. 79:283–289, 1967; Young, Auk 80:145–155, 1963; Holcomb and Twiest, Bird-Banding 39:14–32, 1968; Francis 1971; Robertson, Can. J. Zool. 50:209–222, 1972). Ratios such as young/adult male may vary between areas in relation to different clutch- or harem sizes. Mayfield (Wilson Bull. 73:255–261, 1961; Wilson Bull. 87:456–466, 1975) suggested variation within indices of prefledging survival may be related to including or excluding nests found prior to incubation, while excluding nests eliminates pertinent data. A survey of the literature on red-wings suggests Mayfield's cautions were well founded since only Young (1963) and Caccamise (Condor 1978) stated clearly how their data were treated. Therefore, statistical comparisons of previous work (e.g., Francis 1971) should be viewed with caution.

Table 2

Causes of Prefledging Mortality for Red-winged Blackbirds at Williamstown Lake, New Brunswick, 1976

Cause	Eggs or nestlings lost	% total eggs or nestlings lost
Unhatched eggs	6E[a]	15
Egg predation	7E	17
Climate	3E	7
Unknown	9E	22
Nestling predation	11N[b]	27
Runt disappearance[c]	5N	12
Total	41	100

[a] E = eggs.
[b] N = nestlings.
[c] Designation to describe smallest nestling in clutches of four which failed to keep pace with siblings' growth and subsequently disappeared from the nest.

Mayfield's (1961, 1975) alternative index and daily survival probabilities (which has not been used for red-wings) reduces these difficulties by integrating a measure of time into the calculation. The major assumption required for the technique's use (i.e., that the rates of loss of eggs during incubation and nestlings during nestling period be consistent) can be validated for red-wings by the work of Young (1963) and Robertson (1972). For Williamstown Lake, probabilities of survival may be divided into component parts as follows (see Mayfield [1975] for details): (1) probability of nest (with some contents intact) surviving incubation $1 - (3/85.5)^{12} = 0.652$; (2) probability egg is fertile $1 - 6/40) = 0.85$; (3) partial egg losses $1 - (0/300.5)^{12} = 1$; (4) probability of egg becoming a nestling $a \times b \times c = 0.55$; (5) probability of a nest (with some contents) surviving nestling stage $1 - (3/75)^9 = 0.693$; (6) partial nestling losses $1 - (4/235)^9 = 0.857$; and (7) probability of an egg producing a fledgling $d \times e \times f = 0.329$.

The daily survival probability was the lowest of the three survival estimates derived in this study (33% as compared to 37% and 41% for fledging success and nesting success, respectively). Because of the small sample size from Williamstown Lake, I consider the survival probability calculation to be more accurate since nests found following commencement of incubation were included and the parameter of time has been quantified.

Acknowledgments.—I am grateful to D. M. Keppie for his encouragement and support. J. Rice, W. Threlfall, C. Pennachetti, and N. Williams offered comments and criticisms. The Canadian Wildlife Service, Sackville, New Brunswick, gave me access to the nest record data. Contents of the study were submitted in partial fulfillment of a B.Sc. (Honours) degree, University of New Brunswick, Fredericton, New Brunswick.—Michael D. Rigby, *Dept. Environment, P.O. Box 4750, St. John's, Newfoundland A1C 5T7, Canada.* *Accepted 15 Jan. 1982.*

Wilson Bull., 94(4), 1982, pp. 571–577

Growth, diet, and mortality of nestling Great Blue Herons.—Patterns of growth and development have been described for a number of Ciconiiformes (Owen, Proc. Zool. Soc. London 133:597–617, 1960; Kahl, Condor 64:169–183, 1962; Siegfried, Living Bird 11: 193–206, 1973; McVaugh, Living Bird 14:163–184, 1975; Kushlan, Auk 94:164–167, 1977, Condor 79:31–36, 1977; Werschkul, Auk 96:116–130, 1979). However, growth has not been documented for the Great Blue Heron (*Ardea herodias*) and the diet of nestlings has been reported mainly for inland populations (Kirkpatrick, Am. Midl. Nat. 24:594–601, 1940; Kushlan, pp. 365–369 *in* Wading Birds, Natl. Audubon Soc., 1978). Additionally, only Pratt (Condor 74:447–453, 1972) has provided a partial description and schedule of nestling mortality in this species. In this study, I describe growth during the first month of life, compare growth between years in the same colony and with adult measurements, and fit growth to common growth equations. Also, I describe the diet of nestlings and discuss the timing and causes of nestling mortality in light of current ideas on the adaptive significance of asynchronous hatching and brood reduction.

Study area and methods.—Great Blue Herons were studied on Boot Island (45°08′N, 65°16′W), Nova Scotia, between April and August in 1977 and 1978. This 144-ha island is located in the Southern Bight of the Minas Basin at the mouth of the Gaspereau River. The river mouth provides one of three major foraging areas for the herons. Nests are located 9–12 m above ground in the tops of white spruce (*Picea glauca*). Numbers of breeding pairs decreased from 42 in 1977 to 26 in 1978. Clutch-sizes ranged between four and six with a mode of five eggs in both years. Mean clutch-size was 4.6 and 5.0 in 1977 and 1978, respectively. An average of 2.6 young fledged per breeding pair in 1977 and 3.1 young in 1978.

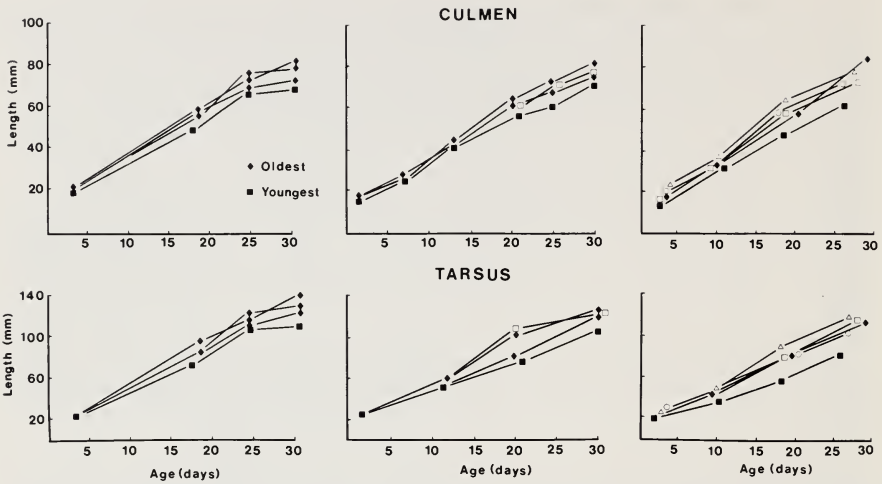


FIG. 1. Growth of culmen and tarsus in three broods of Great Blue Herons. Left: three oldest hatched on same day, youngest hatched 2 days later. Center: two oldest hatched on same day, youngest hatched 7 days later. Right: youngest hatched 5 days after oldest.

Twenty-three and 36 nestlings from 12 and 16 nests in 1977 and 1978, respectively, were measured every 2–3 days. Seventeen of the young measured were the first in their brood to hatch, 13 hatched last, and 29 hatched neither first nor last. Day 0 is considered the day of hatching. To increase sample size, measurements taken on days 0 and 1 were combined to give an average age of 0.5 days. In the same way data from days 28 and 29 were combined to give an average age of 28.5 days. Most nestlings were not handled after the age of 30 days as they may leave the nest and perch precariously when disturbed.

Visits to the colony were restricted to a maximum of 2 h per day. Weather permitting, nest checks were conducted during the morning in 1977. In 1978, they were undertaken during the high tide periods when the island could be visited by boat. Nestlings were lowered to the ground where the following measurements were taken: body weight (using hand-held Pesola spring balances), exposed culmen and tarsal length (to the junction with the base of the middle toe with vernier calipers), wing chord, proximal wing length (the distance from the back of the elbow to the distal tip of the longest primary), and length of the 10th primary from its insertion to its distal tip (with rulers). Colored nail polish and pipe cleaners were used to mark young nestlings individually in 1977 and 1978, respectively. When about 2 weeks old, nestlings were banded with standard U.S. Fish and Wildlife Service aluminum bands.

Adult measurements for *A. h. herodias* were obtained from 63 museum specimens from the National Museum of Canada (Ottawa), Royal Ontario Museum (Toronto), and the American Museum of Natural History (New York).

Some adults and nestlings regurgitated when disturbed or handled. Whenever possible, food items from these regurgitations were identified to species level and their lengths and weights were taken.

Data for growth variables were tested for normality using the Kolmogorov-Smirnov test (STAT PACK V4, Western Michigan University). STAT PACK V4 was also used for regres-

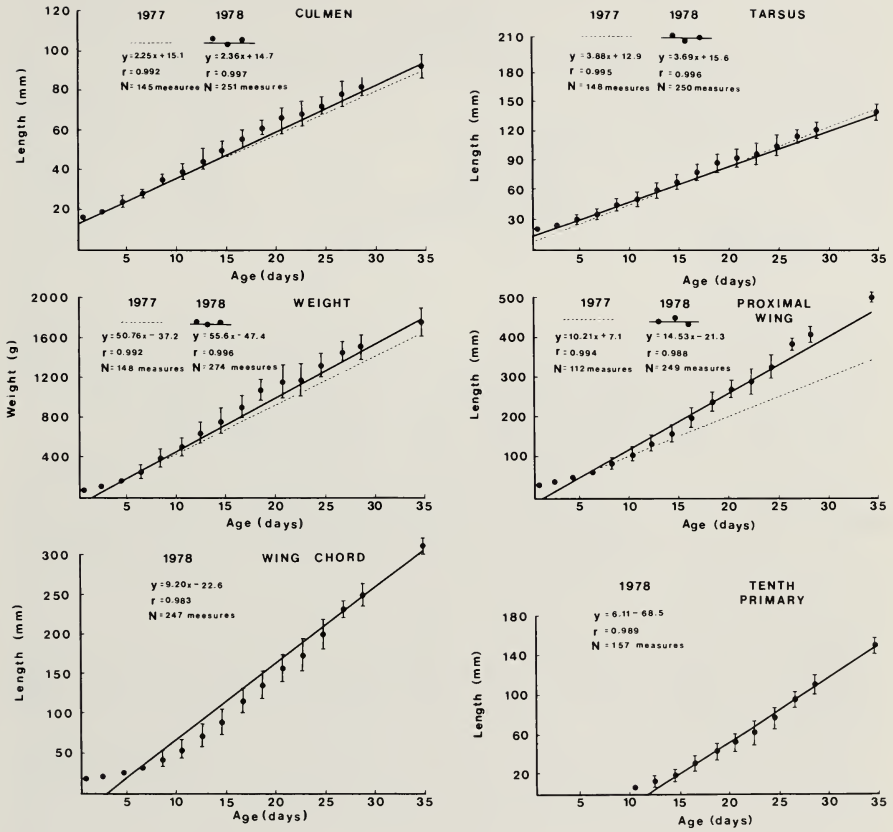


FIG. 2. Growth of nestling Great Blue Herons. An average of 9 and 16 nestlings (1977 and 1978, respectively) were measured at each age. Lines were fitted by regression, and vertical bars represent ±SD for 1978.

sion analysis. Growth measurements were fitted to three common equations—logistic, Gompertz, and von Bertalanffy (Ricklefs, Ecology 48:978–983, 1967).

Nestling growth.—I found that full nestling emergence from an egg whose shell had a star-shaped crack or had a small hole usually took 48 h or less. Although hatching is generally asynchronous (sometimes spread over 7 days), two or more eggs in a clutch may hatch on the same day. The semi-altricial nestlings (Nice, Trans. Linn. Soc. 8, 1962) emerge down covered and are fed by both parents until 2–3 weeks after fledging. Fledging occurs at about 7–8 weeks of age.

Nestlings last to hatch in their respective clutches grew more slowly than those that hatch first (Fig. 1 and Table 1). To compare growth between years I constructed growth curves wherein each age is represented by nestlings from all positions in a brood (Fig. 2). The regression lines thus represent the growth of an "average" nestling.

External sexing of nestlings was not possible. If sexual dimorphism in growth occurs it

Table 1

Culmen Growth of First- and Last-hatched Nestlings

Hatch order	N	Regression equation	*r*	SD[a] (slope)	SD[b] (intercept)
First	17	2.5x + 12.3	0.998	0.04	0.73
Last	13	2.2x + 15.8	0.996	0.05	0.87

[a] $t = 4.28$, $P < 0.001$.
[b] $t = 10.86$, $P < 0.001$.

should become apparent with increasing age. I constructed histograms for culmen and tarsal length, weight and wing chord for all nestlings 28.5 days old (N = 15) from 1978. Bimodal distributions that would suggest dimorphism were not evident for any of these variables. I concluded that no measurable dimorphism in growth occurs up to age 28.5 days.

Correlation coefficients obtained from the regression analysis indicate strong linear relationships between age and all variables measured through the first month of life (Fig. 2). The slopes for weight and proximal wing length differed significantly between 1977 and 1978 ($P < 0.001$) such that changes in body weight and wing length were more rapid in 1978.

Adult measurements.—Measurements of adult Great Blue Herons are given in Table 2. I combined male and female measurements for two reasons. First, a significant difference was found between the sexes only in wing chord length. Second, birds of undetermined sex were frequently encountered in the museum specimens that I examined.

The growth of various nestling body parts is expressed as a percentage of the adult measure in Fig. 3. At 44 days of age (about 1 week prior to fledging), 96% of the adult tarsal length is achieved. Additionally, 86% of the adult body weight, 83% of wing chord length and 78% of the culmen length are attained. Differential rates of growth are also seen in this figure.

Growth equations.—The correlation coefficients obtained for all measured body parts indicate that a simple linear relationship between age and a given part can be used to adequately describe growth through the first 30 days of life. How can growth be best described after the first month of life? Growth measurements were fitted to three common growth equations: the logistic, Gompertz and von Bertalanffy. The standard deviations indicated that the logistic growth curve provided the best fit. However, the predicted asymptote was close to the actual asymptote only for the tarsus. Here, the logistic equation predicted an asymptote 4% below the actual value of 173 mm.

Diet.—Ninety-five piscine food items from six species were identified from regurgitations

Table 2

Measurements of Adult Great Blue Herons from Eastern North America

	N[a]	Mean ± SD	
Culmen (mm)	53	137.1	7.5
Tarsus (mm)	62	173.3	11.5
Wing chord (mm)	63	463.3	15.9
Weight (g)	37	2229.1	762.1

[a] 8–16 males, 10–15 females, sex of others unknown.

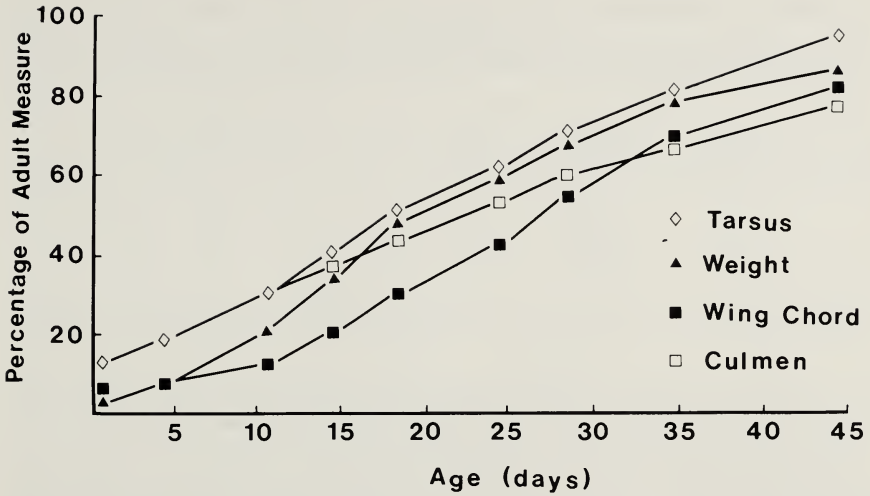


FIG. 3. Growth of nestling Great Blue Herons in 1978 expressed as a percentage of adult measurements. On average, 16 nestlings were measured at each age.

(Table 3). The results show a shift with time in the type of prey species delivered to the nestlings. Owen (1960) reported such a shift for the Grey Heron (*Ardea cinerea*) in England. These changes may be associated with changes in prey availability. Size extremes ranged from 1-g, 46-mm mummichog to a 400-g, 637-mm American eel. Prey of increasingly large size were brought to the nestlings as the season progressed. Small and well digested items were regurgitated by the youngest nestlings and larger, less digested ones by older nestlings. Kirkpatrick (1940) obtained regurgitated prey 50–400 mm in length and 28–398 g in weight from Wisconsin Great Blue Heron nestlings. Hoffman (pp. 365–369 *in* Wading Birds, Natl. Audubon Soc., 1978) found prey in Ohio to range between 78 and 228 mm.

Nestling mortality.—In 1978, 10% of all nestlings in the heronry died before fledging. In

TABLE 3

REGURGITATED FOOD ITEMS OF GREAT BLUE HERONS, 1977–1978

	Atlantic silverside (*Menidia menidia*)	Mummichog (*Fundulus heteroclitus*)	American eel (*Anguilla rostrata*)	Gaspereaux (*Alosa pseudo-harengus*)	Pollack (*Pollachius virens*)	Yellow perch (*Perca flavescens*)
15 May–15 June[a]	25	4	8	8	0	8
16 June–15 July[a]	0	17	11	4	10	0
% total items collected	26	22	20	13	10	8
Mean weight (g)	5	4	95	83	32	12

[a] $\chi^2 = 52.28$, df = 5, $P < 0.001$.

TABLE 4

NESTLING MORTALITY IN RELATION TO AGE AND ORDER OF HATCH, 1977 AND 1978

	Number dead	Age at death (days)	Order of hatch					
			1st	2nd	3rd	4th	5th	last
	22	1–10	1	2	2	1	1	15
	3	11–20	0	0	0	0	0	3
	0	21–30	0	0	0	0	0	0
	5	31–40	0	2	1	1	0	1
Total	30		1	4	3	2	1	19

1977, 16% of the young died. The hatch order and age at death are given for 70% of the dead nestlings in Table 4. Sixty-three percent of those that died were the last to hatch in their clutches. Furthermore, 73% of the nestlings died within their first 10 days of life.

Discussion.—An asynchronous hatch usually results in size hierarchies and differential growth within a brood. This pattern of hatching has been thought to facilitate partial loss of the brood when food supply is restricted. The loss of one or two of the smallest siblings might be preferable to all siblings being affected by food shortage (Lack, Ibis 89:302–352, 1947; Owen 1969; Ricklefs, Ibis 118:179–207, 1976; O'Connor, Anim. Behav. 26:79–96, 1978; Werschkul and Jackson, Ibis 121:97–102, 1979). Hussel (Ecol. Monogr. 42:317–364, 1972) and Bryant (Ibis 120:16–26, 1978) suggest that size hierarchies may spread out the food needs of individual siblings and thus space the demands upon adults. Size hierarchies and brood reduction occur frequently in the nests of Boot Island Great Blue Herons. The youngest nestlings in a given brood grow more slowly and survive less well than their eldest sibling. In those nests for which I have data, the youngest nestling died within 2 weeks of hatching in 19 of 46 nests, and 63% of all the dead nestlings hatched last in their brood. These results clearly show the influence of asynchronous hatching. Siblings are sometimes 7 days apart in age. There is no preferential feeding of the nestlings because the parents feed the young by regurgitating food into the floor of the nest, and aggression between siblings is pronounced at feeding times. The primary cause of nestling mortality appears to be starvation of youngest nestlings because of their failure to compete successfully with older siblings for food. Werschkul (1979) observed the same pattern in the Little Blue Heron (*Egretta caerulea*). On Boot Island mortality decreased after the first 10 days until the nestlings were 5 weeks old. This corresponds to the age that birds begin vigorously exercising their wings and moving out of their nests onto adjacent branches, whereupon some fall. Seventeen percent of the nestlings that died succumbed in this manner.

My results resemble those obtained by McAloney (Can. Field-Nat. 87:137–140, 1973) from Tobacco Island, Nova Scotia. Ninety percent of the Great Blue Heron nestlings that died in his study were the last to hatch. Total nestling mortality on Tobacco Island was 7%. Boot Island mortality was 16% in 1977 and 10% in 1978. In contrast to these Nova Scotia results, Pratt (1972) reported mortality ranging from 19–45% between 1967 and 1970 for Great Blue Heron nestlings in California. Most of the deaths occurred when the young were 4–5 weeks old. Owen (1960) found nestling mortality to be as high as 46% in the Grey Heron, and he stated that it was always the smallest, last-hatched young that died.

Boot Island herons commonly forage in three nearby estuaries. These estuaries are available for foraging at low tide which occurs twice every 24 h. However, weather conditions are far less predictable, and rain and high winds have a detrimental effect upon foraging

success (Bovino and Burtt, Auk 96:628–630, 1979; Quinney and Smith, Can. J. Zool. 58: 1168–1173, 1980). The asynchronous hatch and consequent brood reduction may be a mechanism that enables herons to reproduce successfully in areas with highly variable foraging conditions.

In summary, nestling Great Blue Herons are close to adult size by the time they fledge. Culmen and tarsal growth show much less variation between years than body weight and wing length. Culmen and tarsal lengths are also useful indicators of nestling age. Nestlings that hatch last in their respective clutches grow more slowly and survive less well than those that hatch first, but overall nestling mortality is low on Boot Island.

Acknowledgments.—P. C. Smith provided advice, encouragement, and financial support throughout the study. J. A. Kushlan, D. H. Mock, D. D. Dow, and P. C. Smith kindly reviewed manuscript drafts. I equally appreciate the selfless efforts of the following in the field: S. K. Mainguy, B. N. Miller, J. S. Boates, C. K. Coldwell, R. D. Elliot, P. W. Hicklin, G. R. Milton, R. J. Sowerby, D. F. Lickley, G. L. Hanson, J. M. Porter, D. C. Boersma, and K. R. S. Quinney. The financial support of the National Research Council of Canada, Canadian Wildlife Service, and the Canada Summer Job Corps program are gratefully acknowledged. I also thank J. C. Barlow, H. Ouellet, and R. Browning for access to museum specimens.—T. E. QUINNEY, *Biology Dept., Acadia Univ., Wolfville, Nova Scotia B0P 1X0, Canada.* (Present address: *Zoology Dept., Univ. Western Ontario, London, Ontario N6A 5B7, Canada.*) *Accepted 20 Dec. 1981.*

Wilson Bull., 94(4), 1982, pp. 577–579

Downy Woodpecker sexes select different cavity sites: an experiment using artificial snags.—Primary cavity users such as woodpeckers typically roost and nest in cavities which they have excavated themselves. Secondary cavity users do not dig, but roost and nest in cavities fashioned by other birds (Thomas et al. *in* Wildlife Habitats in Managed Forests, J. W. Thomas, ed., USDA For. Serv. Agric. Handbook No. 553, 1979). This group also readily accepts nest boxes, which has allowed extensive manipulative research into their breeding biology, territoriality, and population regulation (Von Haartman *in* Avian Biology, Vol. 1, D. S. Farner and J. R. King, eds., Academic Press, New York, New York, 1971).

This report introduces artificial snags made of polystyrene as a research tool for manipulating populations of woodpeckers. Habitat selection and phenology of excavation in Downy Woodpeckers (*Picoides pubescens*) using artificial snags will be reported elsewhere (Peterson and Grubb, unpubl.). Here, I address the question, important for future research, whether Downy Woodpeckers as a species have a preferred snag height in which to dig roost cavities.

For primary cavity users, available snags of dead and rotting wood appear to be a resource that limits population density (Short, Wilson Bull. 91:16–28, 1979). Downy Woodpecker sexes have sex-specific foraging niches, presumably in response to limited food resources (Grubb, Condor 77:175–182, 1975; Williams, Am. Midl. Nat. 93:354–367, 1975). Thus, I also attempted to determine whether the sexes might segregate the roost-site resource by showing preference for snags of different height and by digging cavities at different distances from the snag top.

The artificial snags consisted of polystyrene ("bead board") cylinders 22.5 cm in diameter painted dark brown. During Oct.–Dec. 1980, I set out 16 trios of these snags in central Ohio woodlots. I drilled a hole 0.75 m up the middle of each cylinder, then slid it down over a metal fence post driven into the ground, where it was held vertically. Each trio was composed

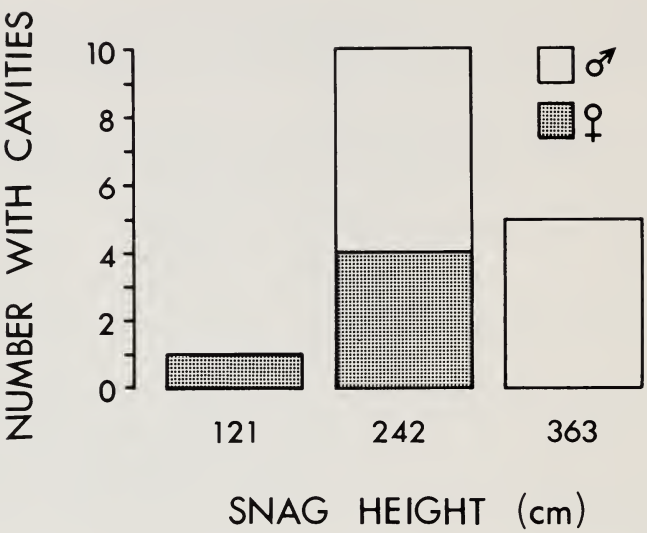


FIG. 1. Heights of artificial snags in which male and female Downy Woodpeckers dug cavities.

of cylinders 121, 242, and 363 cm in length arranged in an equilateral triangle 3 m on a side. Relative positions of snag heights were randomly placed within each triangle. Cylinders were checked daily until I found a completed cavity, defined as an excavation more than 10 cm deep on the vertical axis. I considered a particular bird to have excavated a specific hole if I flushed it from that cavity or noticed it in the immediate vicinity; Downy Woodpeckers defend their cavities (Kilham, Condor 64:126–133, 1962). Five woodlots were used. No two trios of cylinders were closer together than 100 m.

In 10 of 16 cases, Downy Woodpeckers dug cavities in the intermediate (242 cm) snag height (Fig. 1). The bird's choice among the three snag heights differed significantly from random ($\chi^2 = 7.68$, df = 2, $P < 0.05$). Although the sample sizes are small, Fig. 1 suggests that the two sexes preferred snags of different height; females avoided the tallest snag which 45% of the males preferred, and males did not use the shortest snag which attracted one of the females.

The sexes also separated their cavities vertically on the snags; females excavated farther down from the top (Fig. 2). In the 10 cases where both sexes used the same height cylinder (242 cm), allowing a controlled test, the distance from the lower lip of the cavity entrance to the snag top was significantly different ($t = 6.6$, df = 8, $P < 0.001$). The lone female selecting a 121-cm snag dug her cavity near the top (Fig. 2), suggesting there is some minimum excavation height above ground in this species. In one population using natural snags, 1 m was the minimum cavity height recorded (Conner et al., J. Wildl. Manage. 39:144–150, 1975).

Downy Woodpeckers, as a species, seemed to prefer 242-cm cylinders, so artificial snags of about this height might be most effective in future study. Basic aspects of population biology now seem open to manipulation, since excavation substrates of controlled size and composition can be provided in quantity. Artificial trees could also be an important means of restocking primary cavity users on clearcut, selectively cut, and strip-mined land. Wood-

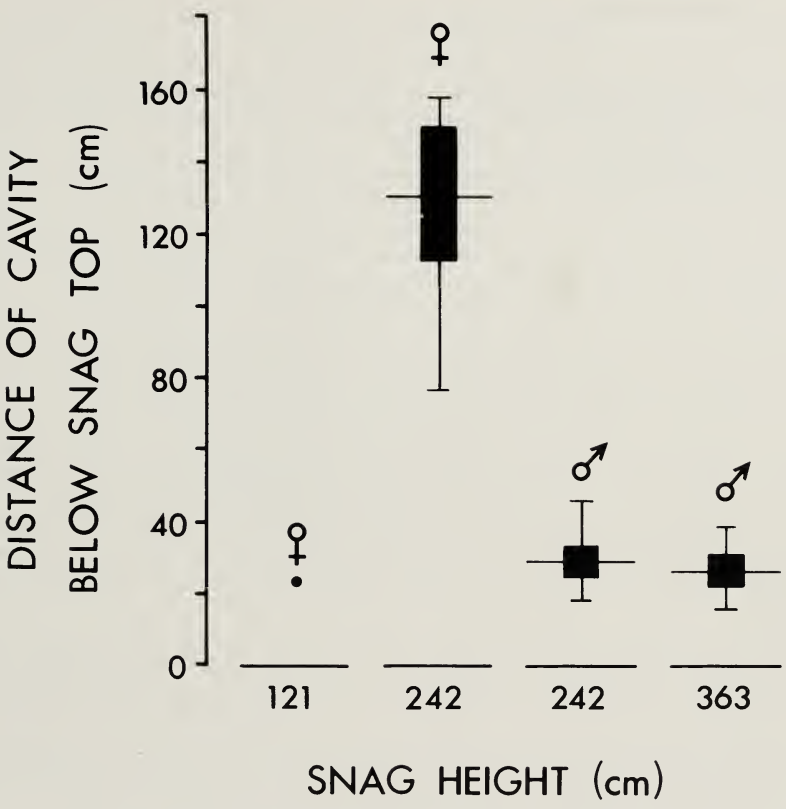


FIG. 2. Distance of cavities dug by male and female Downy Woodpeckers below the top of artificial snags. The horizontal lines are the means, the bars are the standard errors, and the vertical lines are the ranges. Numbers of cavities for each sex are the same as in Fig. 1.

peckers could be attracted to cylinders in such areas, or they could be moved there with their snag after being trapped in it while roosting at night.

These results suggest that Downy Woodpecker sexes segregate along a niche dimension for cavity site. Males preferred taller snags and excavated closer to a snag's top. As snags could be a limiting resource, intersexual roost-site competition may thereby be reduced, allowing the male and female of a pair to remain in close proximity throughout the year.

I thank C. S. Adkisson, R. N. Conner, J. B. Williams, and A. W. Peterson for their comments on earlier drafts, the last also for technical assistance. R. Gifford and the heirs of S. Finkbone permitted use of their woodlands. This research was supported by funds provided by the USDA Forest Service, Northeastern Forest Experiment Station.—THOMAS C. GRUBB, JR., *Dept. Zoology and Environmental Biology Program, Ohio State Univ., Columbus, Ohio 43210.* *Accepted 15 Feb. 1982.*

Wilson Bull., 94(4), 1982, pp. 580–582

A nest of the Pale-billed Antpitta (*Grallaria carrikeri*) with comparative remarks on antpitta nests.—The antpittas (Grallariinae: Formicariidae) are a widespread group in tropical America, yet their breeding biology is poorly known because of their secretive habits. Few antpitta nests have been found, and only Skutch (Life Histories of Central American Birds, III, Cooper Society, Berkeley, California, 1969) has observed the behavior of adult birds at the nest for any appreciable amount of time, and then only during incubation. I here report observations at a nest with young of the newly-described Pale-billed Antpitta (*Grallaria carrikeri*) (Schulenberg and Williams, Wilson Bull. 94:105–113, 1982).

Nest description.—I found the *G. carrikeri* nest in cloud forest at 2875 m, above Cumpang, along the trail to Ongón (8°12′S, 77°10′W), in the Dept. La Libertad, Perú, on 14 October 1979, when I saw an adult carry food to it. The nest was only about 5 m from a trail along which perhaps 30 people with burros pass daily. The nest, on the sloping trunk of a partially fallen tree (0.5 m in diameter), was 3 m vertically above the steeply sloping ground. The nest (LSUMZ nest collection), concealed among living mosses, ferns, and dead leaves on the trunk, comprised a few small sticks and a mass of wet, decaying leaves of the same type found on the trunk. The nest merged almost imperceptibly with detritus on the trunk, so that if the rootlets lining the cup had not been seen, the nest would have been difficult to distinguish. Approximate outer measurements were 20 × 19 cm, and the inner dimensions of the cup were 14 × 12 cm, by 5 cm deep. No eggshell fragments were found in or around the nest.

Behavior at the nest.—M. B. Robbins and I took notes on the behavior of the adult antpittas at the nest for a combined total of about 11 h on 14 and 15 October 1979. Both adults participated in feeding and brooding the nestlings. Several times I saw both adults at the nest simultaneously, when one adult replaced the other in brooding. Skutch (1969) noted that in the Streak-chested Antpitta (*Hylopezus perspicillatus*) both adults also participate in incubating the eggs. Both *G. carrikeri* nestlings were fed each time that an adult returned to the nest, on the average about every 30 min. Frequently, however, a period of 1 h or more passed without a visit to the nest, followed by two feeding visits in a few minutes. After feeding the young birds, the adults often reached down into the nest and appeared to be eating something that I never could see. Since no removal of feces was observed, and since the nest was very clean when I collected it, I assumed the adults were eating the nestlings' fecal sacs.

Invariably after feeding the young, the adults began brooding them. Neither adult brooded more than 41 min at one time ($\bar{x}$ = 27 min, N = 14). The nest was covered by an adult 6.6 h of our 11 h of observation (60%). The weather during this period was cool and cloudy, but no rain fell, and temperature extremes were a daytime high of 23°C, and a nighttime low of 10°C on the 14th and 11°C on the 15th.

Although food items brought to the nest were difficult to identify, earthworms (Annelida) seemed to be an important part (7 of 19 feedings) of the nestling diet. However, earthworms seemed to be an uncommon food for the adults themselves. Although one male (LSUMZ 92460), which was eventually collected when it brought food to the nest, was found to have a portion of an earthworm (3 cm long) in its stomach, no other individuals collected in this area had earthworm parts in their stomachs.

Unlike the Streak-chested Antpitta observed by Skutch (1969), the Pale-billed Antpitta never called from the vicinity of the nest, although its distinctive call (see Schulenberg and Williams 1982) was heard frequently in mid-mornings elsewhere in the forest.

Nestlings.—The nestlings were estimated to have been about 7 days old when collected (LSUMZ 91513 and 91514). They weighed 27 and 26 g, respectively. Their eyes were not yet

open and down was sparse. An egg tooth was still present. The bill and mouth lining were bright orange.

Nesting in the Grallariinae.—Nests have been reported for only 11 of 41 species in the subfamily Grallariinae (following the taxonomy of Lowery and O'Neill, Auk 86:1–12, 1969), but those reported show many similarities. The clutch-size found in all nests reported so far (23 of 25) is two, except for one clutch of three collected by S. B. Gabaldon (American Museum of Natural History 13865, J. Bull, pers. comm.) from a Chestnut-crowned Antpitta (*Grallaria ruficapilla*) nest, and one nest of Scaled Antpitta (*G. guatimalensis*) with only one egg (Edwards and Lea, Condor 57:31–54, 1955).

Although antpittas seem to be largely terrestrial, their nests are generally placed above ground, but usually not more than 3 m above the forest floor. Edwards and Lea (1955) and Rowley (Proc. Western Foundation of Vertebrate Zool. 1(3):1–204, 1966) reported *G. guatimalensis* nests found close to the ground placed on top of fallen trunks. Belcher and Smooker (Ibis 6:792–813, 1936), however, found a *G. guatimalensis* nest 2.4 m above the ground. The Pale-billed Antpitta nest described above was about 3 m vertically above the ground, but only about 1.5 m from the base of the steeply sloping trunk upon which it was placed.

A common nest-site for antpittas is on top of fallen or partially fallen trunks, as the nests described above. A few nests have been found in low, understory bushes or vines. Miller (Univ. Calif. Publ. Zool. 66:1–78, 1963) reported a *G. guatimalensis* nest among the branches of a fallen shrub, and Skutch (1969) described a *H. perspicillatus* nest suspended in the branches of a low bush. *Hylopezus perspicillatus* has also been recorded building in vine tangles (Willis and Eisenmann, Smithson. Contrib. Zool. 291, 1979). Schwartz (Boletín Sociedad Venezolana de Ciencias Naturales 88:42–62, 1957) found four nests of the Rusty-breasted Antpitta (*Grallaricula ferrugineipectus*), all in low bushes or vine tangles. A pair of Rufous-faced Antpittas (*Grallaria erythrotis*) built a nest in tropical foliage at the New York Zoological Park (Bell and Bruning, Avicul. Mag. 82:119–122, 1976), but the normal, preferred nest-site may not have been available to those birds.

Antpittas also build nests among the rosettes of leaves formed by palms and aroid plants. Wetmore (Birds of the Republic of Panamá, Pt. 3, Smithsonian Institution Press, Washington, D.C., 1972) found a Black-crowned Antpitta (*Pittasoma michleri*) nest in the crown of a low palm. The nest of *G. guatimalensis* found by Belcher and Smooker (1936) was placed at the heart of an aroid growing on a tree trunk. A. Williams found two nests of *H. perspicillatus* (Western Foundation of Vertebrate Zoology 58259, 58404; L. Kiff, pers. comm.) in the centers of rosettes of unidentified plants.

The nests reported have varying dimensions, but all are described as roughly circular, shallow cups, usually 6 cm deep or less, usually lined with fine rootlets or vegetable fibers. The main body of the nest is generally composed of a loosely constructed, thick mass of leaves, often wet and decaying, that can hardly be distinguished from surrounding leaf litter or debris.

Eggs of *Grallaria* spp. are pale blue or blue-green (Schönwetter, Handbuch der Oölogie, Vol. 2, Pt. 14, Akademie-Verlag, Berlin, Germany, 1967), except for the set from *G. ruficapilla*, which has buffy eggs with rufous blotches (J. Bull, pers. comm.). When the eggs of other species in the same subgenus (*Hypsibemon*) as *G. ruficapilla* are known, it will be interesting to see if egg coloration is a subgeneric character.

Known eggs of small antpittas in the genus *Grallaricula* are light coffee-brown with darker brown blotches (Slate-crowned Antpitta [*G. nana*] and Hooded Antpitta [*G. cucullata*]) (Schönwetter 1967), although the ground color of *G. ferrugineipectus* is light green (Schwartz 1967). *Pittasoma michleri* also has brown-blotched eggs, but with a "pinkish-buff" background (Wetmore 1972). Eggs of *H. perspicillatus* have a more varied background color (light gray [Skutch 1969], pale olive-buff [Wetmore 1972], or yellowish-brown [Schönwetter 1967]), but they too have dark brown blotches.

Acknowledgments.—I am grateful for the financial support of the Peruvian fieldwork by Babette M. Odom, John S. McIlhenny, Edmund W. Mudge, and H. Irving and Laura R. Schweppe. The fieldwork was also facilitated by colleagues of the Dirección General Forestal y de Fauna of the Ministerio de Agricultura in Lima. I also appreciate information provided by Lloyd F. Kiff (Western Foundation of Vertebrate Zoology) and John Bull (American Museum of Natural History) on antpitta nests and eggs under their care. I thank J. V. Remsen, M. B. Robbins, T. S. Schulenberg, F. G. Stiles, M. D. Williams, and E. O. Willis for comments on the manuscript. I acknowledge the continued collaboration of Aero Perú.—
David A. Wiedenfeld, *Museum of Zoology, Louisiana State Univ., Baton Rouge, Louisiana 70893.* *Accepted 26 Jan. 1982.*

Wilson Bull., 94(4), 1982, pp. 582–584

Interspecific nest use by aridland birds.—Nest holes drilled by woodpeckers (Picidae) are frequently used by secondary cavity-nesting species, but interspecific use of open and domed nests is less well known. Nests constructed by many southwestern desert birds last longer than one year (pers. obs.) and are consequently reused by the same pair (e.g., Abert's Towhees [*Pipilo aberti*], pers. obs.) or by other birds as suitable nests. I observed several instances of interspecific nest use in honey mesquite (*Prosopis glandulosa*) habitat of the lower Colorado River valley, on the Colorado River Indian Reservation about 10 km north of Ehrenberg, Yuma Co., Arizona.

On 25 March 1980, I discovered a Mourning Dove (*Zenaida macroura*) incubating two eggs in a Crissal Thrasher (*Toxostoma dorsale*) nest built at a height of 130 cm against the main trunk of a 4.6 m honey mesquite. The nest tree was on the border of a thick mesquite woods adjacent to a large opening of bare ground. I had observed a pair of Crissal Thrashers incubating four eggs in this same nest during the summer of 1979. On 5 April 1980, the nest contained one dove egg that had been abandoned. Secondary use by Mourning Doves of nests of other bird species has been reported to be as frequent as 27% in Tennessee (Monk, Migrant 20:1–9, 1949) and is common throughout North America (e.g., McClure, Trans. N. Am. Wildl. Conf. 15:335–343, 1950; Cowan, Calif. Fish and Game 38:505–521, 1952; Nickell, Wilson Bull. 66:137, 1954; Hanson and Kossack, Illinois Dept. Conserv. Tech. Bull. 2, 1963). Documented use of secondary nests by doves in the southwest is limited. One Mourning Dove nest with two eggs, found by J. C. Barlow (pers. comm.), was built on top of an abandoned Cactus Wren (*Campylorhynchus brunneicapillus*) nest in a cholla (*Opuntia* sp.).

On 16 June 1980, I found a female Abert's Towhee incubating two eggs in the Crissal Thrasher nest mentioned above. I had color banded this towhee in the spring of 1980 and observed four of her previous attempts to nest. Two earlier nests were built in mistletoe (*Phoradendron californicum*) (a parasite of mesquite) and the other two nests were built directly on honey mesquite branches. The nest heights ranged from 0.92–2.3 m. On 10 June 1980, the fourth of these nests, which contained one egg recently laid by the towhee and one egg of a Brown-headed Cowbird (*Molothrus ater obscurus*), fell to the ground. The female towhee laid a fifth clutch of two eggs in the thrasher nest about 90 m south of her fourth nest tree.

During the spring and summer of 1980, I found three additional clutches of Abert's Towhees in old Crissal Thrasher nests. I had observed construction and use of these nests by three pairs of Crissal Thrashers in the spring of 1980. One pair of thrashers fledged three young, but the nests of the other two pairs were depredated, possibly by snakes or Roadrunners (*Geococcyx californianus*) (e.g., Finch, Condor 83:389, 1981) without damage to the nests.

In contrast to the large stick nests of thrashers, the towhee nests (N = 68) were constructed of fresh mesquite leaves and bark, salt cedar (*Tamarix chinensis*), saltbush (*Atriplex lentiformis*), inkweed (*Suaeda torreyana*), and/or arrowweed (*Tessaria sericia*) leaves, grasses, and even newspaper. The four towhees that used thrasher nests relined the nests with fresh grass and modified the exterior by weaving green leaves into the original stick structure. I followed the nesting histories of 12 color-banded Abert's Towhee females and found that the four towhees mentioned above only laid clutches in thrasher nests after previous nesting attempts in nests that the towhees had built had failed.

Nesting mortality of Abert's Towhees was high in 1980, and towhees that renested after failure reduced the time allocated to construction of second and later nests (Finch, M.Sc. thesis, Arizona State Univ., Tempe, Arizona, 1981). Towhee parents could consequently invest more time directly into offspring care before the favorable period for breeding ended. Towhees that could find and use thrasher nests may have increased their chances of renesting successfully by avoiding delay in nest construction. Towhees may have used only Crissal Thrasher nests because they were the only nests in the area similar in size to towhee nests.

The bulky, stick nests of Crissal Thrashers are durable, highly visible, and probably easily found as are the domed nests built by Cactus Wrens and Verdins (*Auriparus flaviceps*). On 28 May 1980 I discovered three Ash-throated Flycatcher (*Myiarchus cinerascens*) nestlings and one egg in an old Cactus Wren nest. The roof of the nest had partially collapsed. The nest was built near an Emlen line transect (used by personnel of the Center for Environmental Studies, Arizona State University) and three censusers had reported seeing wrens using it in 1977 and 1978. Ash-throated Flycatchers nest in woodpecker holes, nest boxes, and natural tree cavities (Bent, U.S. Natl. Mus. Bull. 179, 1942; Scott et al., Agric. Handbook 511, 1979). Experimental manipulations of the number of nest holes available in honey mesquite habitat indicate that nest-sites may be limiting for secondary-cavity nesting passerines in the Colorado River valley (Brush, M.Sc. thesis, Arizona State Univ., Tempe, Arizona, 1981). Because the large, roofed nests of Cactus Wrens provide enclosed cavities, they may be used as nest-sites by Ash-throated Flycatchers when tree holes are unavailable.

The Black-tailed Gnatcatcher (*Polioptila melanura*) is known strictly as an open-nest species. On 15 April 1980, I was attracted by the activities of a gnatcatcher pair. I found a Verdin nest in a mesquite nearby, but no gnatcatcher nest. The gnatcatchers began "buzzing" loudly, however, and the male scolded me while he was perched on the Verdin nest. Using a mirror mounted on a pole, I examined what should have been the roof of the Verdin nest. I found instead a compact gnatcatcher nest made of spider webs and salt cedar seeds centered within the dry twig shell of the Verdin structure. The nest was empty. Over the following week, the birds completely dismantled their nest, until only the circular casing of the Verdin nest was left. I did not locate the new gnatcatcher nest.

A wide variety of open-nesting species use nests built by other birds (e.g., Parmelee, Loon 51:169–170, 1979; Butler, Can. Field-Nat. 94:197, 1980; Hammerson and Lapin, Wilson Bull. 92:511, 1980; for extensive reviews, see Roberts, Emu 55:110–126, 173–184, 1955; Skutch, Parent Birds and Their Young, Univ. Texas Press, Austin, Texas, 1976:128–129). There are few records, however, of secondary nest use by southwestern desert birds. My observations indicate that open-nesting aridland birds also use the deserted nests of other species. Using secondary nests may save time and energy (e.g., Mourning Doves, Abert's Towhees), occur when nesting material or nest-sites are unavailable or in short supply (e.g., Ash-throated Flycatchers), or possibly serve as an added measure of brood protection against radiant heat, wind, or cold.

I thank S. H. Anderson, D. B. Inkley, R. T. Reynolds, and D. E. Runde for reviewing this note. Observations were made while I was a graduate student in the Dept. Zoology at Arizona State University.—Deborah M. Finch, *Rocky Mountain Forest and Range Exper-*

iment Station, Arizona State Univ., Tempe, Arizona 85281. (Present address: *Forest, Range and Watershed Laboratory, 222 South 22nd Street, Laramie, Wyoming 82070.*) *Accepted 2 Jan. 1982.*

Wilson Bull., 94(4), 1982, p. 584

An apparent instance of communal nesting by American Oystercatchers.—Communal nesting, as defined by Van Tyne and Berger (Fundamentals of Ornithology, John Wiley and Sons, New York, New York, 1976), is known from a few species in widely divergent orders. I observed a communal American Oystercatcher (*Haematopus palliatus*) nest on the Laguna Madre that represents the first published record of communal nesting for the species.

On 4 June 1977 I found an American Oystercatcher nest on Dimmit Point Island, located at the junction of the Laguna Madre and Corpus Christi Bay, Nueces Co., Texas. The nest, situated atop a shell embankment 1 m high, and on the periphery of a Black Skimmer (*Rynchops niger*) colony, contained six eggs. Four adult oystercatchers flew near me, calling, while I photographed the nest.

The following morning I again visited the island and concealed myself in salt cedar (*Tamarix* sp.) bush 400–600 m from the nest. During the course of the morning, all four oystercatchers remained in the vicinity of the nest, rarely straying more than 100 m away. Three of the oystercatchers entered the nest and sat on or turned the eggs, although none remained in the nest for more than 10 min. The eggs hatched sometime during the following week, for on 15 June I briefly observed four young on the island in the vicinity of the nest. When my presence was detected, the young hid in low vegetation and three adults flew around me calling.

According to Bent (U.S. Natl. Mus. Bull. 142, 1929: 307), the normal clutch-size for American Oystercatchers is three eggs. However, Bent mentions that clutches of five and six eggs have been found. This apparent instance of communal nesting is exceptional among 21 other American Oystercatcher nests that I have located along the Texas coast since 1973, each being an isolated nest with a two- to three-egg clutch.—Brian R. Chapman, *Dept. Biology, Corpus Christi State Univ., Corpus Christi, Texas 78412. Accepted 10 Feb. 1982.*

Wilson Bull., 94(4), 1982, pp. 584–585

Song Sparrow pair raise four broods in one year.—Temperate zone passerines are often double-brooded (e.g., Bryant, J. Anim. Ecol. 48:655, 1979) and occasionally raise up to three broods per year (e.g., Snow, A Study of Blackbirds, George Allen and Unwin, London, England, 1958). Cases where four broods are raised, however, are extremely rare, although there are records of three broods being raised and a fourth clutch being unsuccessful (Weaver, Auk 60:62, 1943; Seel, Ibis 110:129, 1968). I report here such a case for the Song Sparrow (*Melospiza melodia*).

Song Sparrow breeding was studied on Mandarte Island, British Columbia, Canada, from 1975–1979 (Smith, Condor 83:152, 1981) and in 1981, when 20 pairs bred on the 6.3-ha island. All breeding adults were color-banded and almost all young were color-banded as nestlings about 6 days after hatching.

One pair of experienced birds, a 3-year-old female and a 7-year-old male, raised four broods in 1981. Clutches of three, four, four, and three eggs were begun on 18 March, 16 April, 14 May, and 14 June, respectively. The final clutch also contained two Brown-headed Cowbird

(*Molothrus ater*) eggs. The first clutch was the earliest ever recorded for this population (Tompa, Ann. Zool. Fenn. 3:3–73, 1964; Smith et al., Oecologia 47:164, 1980).

A simple model of the temporal spacing of Song Sparrow broods (Smith and Roff, Can. J. Zool. 58:1007, 1980) shows that a brood-size of one is the only one that will allow Song Sparrows sufficient time to raise four broods, except in an unusually long breeding season. This was precisely the situation for this pair. Only a single sparrow-young reached banding age in each of the first three broods. Because the parents had previously bred together this may have allowed broods to be more closely spaced in time (Smith and Roff, 1980). The final nesting attempt of the pair raised both cowbirds and two of the Song Sparrows to banding age. In all, the four nests fledged at least five Song Sparrows and one cowbird (as judged from begging calls of fledged young), and at least two of the young sparrows reached independence from parental feeding. Thus, the pair were able to compensate for the extreme brood reduction in their first three nests and still have a moderately successful breeding season.

No other pair raised four broods of young in a single year during 6 years of intensive study. Nice (Trans. Linn. Soc. New York 4:93, 1937) cited a report of a single case where a pair of Song Sparrows raised four broods in Ohio. This pair also began the four broods at intervals of about 4 weeks, but began to breed almost 6 weeks later than the case reported here. I doubt if attempting to raise four broods constitutes a breeding "strategy" in the Song Sparrow or other temperate zone passerines. Rather, it is a consequence of having three small broods at the start of the breeding season.

I thank the Natural Sciences and Engineering Research Council of Canada for financial support, and the Tsawout and Tseycum Indian Bands for allowing me to work on their island.—James N. M. Smith, *Dept. Zoology, Univ. British Columbia, 6270 University Blvd., Vancouver, British Columbia V6T 2A9, Canada.* *Accepted 2 Apr. 1982.*

Wilson Bull., 94(4), 1982, pp. 585–590

Post-copulatory display in the Lark Bunting and other species.—In the summer of 1964, Lark Buntings (*Calamospiza melanocorys*) unexpectedly nested in large numbers in southern Saskatchewan and other regions remote from their usual range (e.g., southwestern Minnesota; Anderson and Getman, Loon 37:63–69, 1965). (For a good description of the habitat used by buntings in the Regina area see Smith and Smith, Blue Jay 24:129–131, 1966.)

Having been intrigued by a post-copulatory display in the male Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) in response to a female dummy of the same species in precopulatory pose (Nero, Wilson Bull. 75:391–394, 1963) I set out to test for this behavior in the Lark Bunting. Tests involving the use of a dummy female Lark Bunting placed on the ground in precopulatory or soliciting pose were carried out at several sites from 24–26 June, and 1 and 8 July 1964. The female dummy was arranged in typical passerine soliciting posture, i.e., head drawn back with bill up and open, tail closed and raised, wings partly out, and body low on the tarsi (see Fig. 1).

No attempt was made to quantify the results: I simply wanted to observe and photograph the results of the tests. The most striking response consisted of a post-copulatory display by the male during which it assumed a static exaggerated version of female passerine precopulatory posture (Figs. 1, 2). Nearly identical displays were given by approximately 20 individual males in response to the same dummy.

The dummy female was first placed in the territory of a male, about 4 m from a nest which

FIG. 1. Male Lark Bunting responding to female Lark Bunting dummy (mounted bird) in typical passerine sexual solicitation posture. Male is in post-copulatory static pose. (Photos reproduced from color transparencies by the author.)

contained four eggs. Two types of response to the dummy were observed: that of the nesting female, and those of her mate and several other males attracted to the scene. Interactions between males were also observed. The female's response gave some indication of conflicting motivations: with feathers sleeked, head held high and legs extended, she approached and attacked the dummy, then suddenly gave an extreme tail-lifting display in what I assumed was appeasement. When the incubating female left the nest to approach the dummy, her mate flew to her with wings raised and tail spread, an aggressive response. In turn she bit him on the head and/or the wing, and briefly held onto him.

At least six other males appeared sexually aroused by the dummy, as indicated by prominent cloacal protuberances. They bill-tilted (indicating threat) and tail-raised (indicating appeasement) to each other, but did not approach the dummy. On the other hand, the response of the territorial male to the dummy was startling. He rushed in, bit at her wing feathers, copulated, then hopped off and demonstrated extreme tail-lifting as he turned away. He disappeared in the grass in silence, but a moment later he emerged, began picking up grass stems until he had a beakful, dropped them and again rushed to the dummy and repeated the performance. After copulating with the dummy three times, however, the male went away with tail lowered and spread. At some time during this sequence semen was deposited on the back of the dummy.

The post-copulatory behavior of males in several other tests with the dummy was variable, showing various degrees of conflict between aggression and appeasement, but exhibiting strong, exaggerated resemblances to the female precopulatory display. The most surprising aspect was the absolute stillness of the bird. Although I had previously seen this in the male Yellow-headed Blackbird it was even more striking here. In extreme display the tail was

FIG. 2. Male Lark Bunting in extreme post-copulatory posture. White eye-ring is anomalous.

straight up (Fig. 1) or even directed forward (Fig. 2), the head withdrawn and the beak up and open (but with no apparent vocalization). At times the nictitating membrane closed and opened. The bird rested on its tarsi, breast to the ground (Fig. 2) and the closed wings were held out. Occasionally, the breast was lowered to the ground even when the male was only half-crouched (i.e., tarsi not resting on the ground). At times the display was so extreme the male appeared to be trying to touch the back of its head with its tail. Similar displays were even given when the dummy was fastened to fence wire, the responding male displaying despite the awkward perch (Fig. 3). Also, there was often a lateral display, the male leaning to one side away from the dummy, keeping the leg on that side partly extended while resting on the opposite tarsus (Figs. 2, 4). During lateral display the wing on the side facing the dummy sometimes was partly spread, and the flank feathers on that side were fanned out (Fig. 2). With its raised bill open, the male's pink-colored palate was conspicuous.

Generally, the more frenzied or hurried the movements of a male approaching the dummy and the more "complete" the copulation effort, the more extreme the post-copulatory display. Often the male approached the dummy in a low run, body and head parallel and low, plumage loose and full, raising the crown feathers (denoting apprehension) as it neared the dummy, then, during copulation, lowering the crown and compressing the head and neck plumage. Occasionally, an approaching male hopped by dropping onto its tarsi, bobbing up and down. The hopping part of the approach sequence was once briefly given by a male responding to a live female. A few times males gathered nesting material prior to approaching the dummy, and once a male copulated while holding long grass stems in its bill. On one occasion a male ran towards the dummy with a weed stalk four times the length of its body held sideways in its bill. Once I saw a live female in precopulatory display holding grass stems in her bill.

FIG. 3. Male in post-copulatory display on fence wire; female dummy to right.

In the summer of 1964, I set up a dummy female Chestnut-collared Longspur (*Calcarus ornatus*) near Moose Jaw, Saskatchewan (G. M. Fairfield's study area), in precopulatory position on the territory of a male of this species which elicited extreme post-copulatory display from the male. Fairfield notes (pp. 1638–1639 *in* Life Histories of North American Cardinals, Grosbeaks, Buntings, Towhees, Finches, Sparrows, and Allies, Austin, ed., Dover, New York, New York, 1968): "Approaching the dummy female in a zigzag course, he erected his chestnut collar, stretched his head high, and looked down at her over his lowered bill from directly in front. He then fluttered to her back and attempted to copulate. Dismounting, he ran away from her holding his body level with the ground, wings and wide-fanned tail almost dragging. He then circled back and tried once more to copulate, and circled to the front. There he assumed an exaggerated 'female precopulatory posture', in which he raised his closed tail as high as possible until his chest almost touched the ground, bent his head back on his shoulders with bill pointing straight up, and the wings projecting back and down."

On 8 May 1966, a display resembling that of the Lark Bunting and the Chestnut-collared Longspur was observed in McCown's Longspur (*C. mccownii*) which occurred briefly but distinctly in post-copulatory response to a dummy male of the latter species (I had been unable to obtain a female). The dummy, in head-up, tail-up posture, was propped up on a McCown's Longspur territory near Regina. As with the Lark Bunting and the Chestnut-collared Longspur, cycles of behavior were observed in which the responding bird several times approached frenziedly, displayed with head held high and crest raised, uttering a high-pitched trill, copulated, went into post-copulatory display close beside and parallel to the dummy, then ran off to "rest." The approach display was given at some distance, gradually

FIG. 4. Male in lateral post-copulatory display (in part); female to right.

building up in intensity, whereupon the male would make his approach, etc. On nearly all of approximately six occasions, the approach was performed with one wing raised straight up, a posture previously noted by DuBois in 1937 (pp. 1576 *in* Austin, ed., 1968). While resting, a double note *chip-peet* was given repeatedly. Usually, post-copulatory display was given to the dummy with the male in a parallel position, lying on its opposite side while maintaining the head-up, tail-up aspect. Often the male ended the rigid post-copulatory display with a spring into the air (from resting on its tarsi) coming down to land on its toes with its wings out. Then the male would walk away with the tail spread (especially on the side nearest the dummy) and the wing on the dummy side highest, at times with a peculiar "scooter-gait," one foot pushing along ahead of the other. Then it would circle in front of the dummy and re-mount, or go away with tail display and wing (or wings) elevated. In these instances what appeared to be annoyance-pecking at the dummy was noted. This has been seen in nearly all my experiments with female dummies (including those involving the Red-winged Blackbird [*Agelaius phoeniceus*] in which no post-copulatory display was ever elicited). Once the McCown's Longspur pulled at rump feathers, and thus dragged the dummy backwards.

Post-copulatory display in the Yellow-headed Blackbird (Nero 1963) included elevated tail, an exposed cloacal area (enhanced by a circlet of yellow feathers), wings held out sideways, and static posture, although head-up display was not given. Tail raising in this species is also given to other males where it is considered an appeasement display. Similar display occurs in several other icterids.

In all likelihood, the head-up, tail-up post-copulatory display by male birds is used in agonistic situations relating to the constant solicitation display of the dummy female. Aspects of the display, especially tail-up, while facing away from an opponent, suggest a high degree of appeasement function in agonistic circumstances.

Performance of head-up, tail-up display in flight by a male Indigo Bunting (*Passerina cyanea*) towards a human supports the suggestion of the use of female solicitation behavior by males under stress in agonistic situations. On 10 July 1971, near East Braintree, Manitoba, both members of a pair of Indigo Buntings appeared and reacted to me as if they had fledglings in the vicinity. Several times when I "pished," the male flew toward me in stilted flight, head and tail up, wings held partly open at the sides and fluttering.

Marler (Behaviour Suppl. 5, 1956:118) described use of the female precopulatory or soliciting posture by male Chaffinches (*Fringilla coelebs*) when confronted by dominant males. The postures of the submissive birds were "identical with the high intensity soliciting posture of the female." Judging from the photos of the latter display, Marler's (1956) submissive males had postures nearly identical to that of Lark Buntings in post-copulatory display. The use of female soliciting posture by male Chaffinches was "associated with a strong escape tendency that is prevented from expression" (Marler 1956:119). Marler (1956:121) notes further that in male-male confrontations "the most elaborate display is associated with the highest intensity of conflict." The post-copulatory display of the Lark Bunting, Chestnut-collared and McCown's longspurs appears to be of this nature. Although elicited by an artificial stimulus source (the dummy bird) these displays must be regarded as a genuine part of the behavioral repertoire of the species, significant in terms of motivation, latent with meaning, and beautiful.

I wish to thank L. Baptista, L. Best, and J. C. Barlow for their comments on earlier drafts.—Robert W. Nero, *Manitoba Wildlife Branch, Box 14, 1495 St. James St., Winnipeg, Manitoba R3H 0W9, Canada.* *Accepted 9 Feb. 1981.*

Wilson Bull., 94(4), 1982, pp. 590–594

Responses of Black-capped Chickadees to mirrors.—The use of mirrors is of interest in studying agonistic and social behavior (Svendson and Armitage, Ecology 54:623–627, 1973). Several species of birds have been tested in the laboratory (e.g., Zebra Finch [*Poephila guttata*], Ryan, Wilson Bull. 90:295–297, 1978; House Sparrow [*Passer domesticus*] and Budregriar [*Melopsittacus undulatus*], Gallup and Capper, Anim. Behav. 18:621–624, 1970). The only species of free-living birds that have been presented with mirrors are Glaucous-winged Gulls (*Larus glaucescens*) (Stout et al., Behaviour 34:29–41, 1969) and Blue Grouse (*Dendragapus obscurus*) (Stirling, Can. J. Zool. 46:405–408, 1968).

Here we examine reactions to mirrors of free-living Black-capped Chickadees (*Parus atricapillus*) in winter flocks. We asked the following questions: (1) How do chickadees respond to mirrors? (2) Do responses reflect differences in dominance rank?

In winter Black-capped Chickadees live in small flocks and exhibit a linear dominance hierarchy (e.g., Glase, Living Bird 12:235–267, 1973). Displays associated with aggressive interactions include various postures, gaping, and a vocalization termed the "gargle" (Ficken et al., Auk 95:34–48, 1978). In natural encounters only the more dominant males give this vocalization frequently.

Experiments were conducted at the University of Wisconsin–Milwaukee Field Station, Saukville, Ozaukee Co., Wisconsin, from January to March 1979. Observations were made from blinds located 10 m from two feeders, D7 and F9. The two feeders were identical in

Table 1

Results of Mirror Experiments at D7 Feeder

Individuals[a]		No. visits in which seeds were taken				No. seeds/visit mirror[b]	No. visits when threats given to mirror
		baseline	mirror	baseline	foil		
PCAO	♂	3	0	1	0	0 (5)	—
JACO	♂	12	7	9	6	0.44 (16)	2
AOYR	♂	9	0	10	0	0 (11)	—
ASYO	♂	3	2	1	4	1 (2)	—
WYAO	♂	12	3	17	2	0.15 (20)	3
AOJJ	♂	5	0	10	5	0 (4)	—
AOCR	♂	2	1	0	0	0.5 (2)	1
ROJA	♂	1	0	0	0	0 (6)	—
AOCC[c]		10	11	13	1	0.5 (19)	—
ABPO	♂	0	0	0	0	0 (3)	—
WBAO	♂	2	0	21	5	0 (5)	—
BOAB[c]		0	0	7	3	0 (1)	—
RSAO	♀	1	2	0	0	0.33 (6)	—
YCAO	♀	30	0	17	2	0 (12)	—
PABO[c]		8	0	3	2	0 (8)	—
RGAO	♀	12	0	11	3	0 (4)	—
RAGO	♂	3	0	0	0	0 (3)	—

[a] Listed in order of dominance.
[b] Total number of visits in parentheses.
[c] Sex unknown.

design but separated by about 100 m. Several flocks visited each feeder. The feeders had two perches but only one bird fed at a time. The chickadees were individually color banded.

Two mirrors were used in the experiments, both 15.2 cm in diameter, but one was covered with aluminum foil so that while a shiny and novel object was presented, a bird could not see its image. For each presentation one of the two "mirrors" was placed in the feeder near the sunflower seeds so that an approaching bird would be confronted by it. Each feeder received three presentations of each "mirror" in random order, at intervals of 1 week (to reduce habituation). Prior to any presentation a 15-min baseline sample of behavior was obtained that included a recording of the number of times the feeder was visited by each individual and whether food was obtained. The mirror or foil was placed in the feeder for 15 min following the baseline and the same data were recorded. Data and vocalizations were recorded on a Uher 4200 tape recorder using an Electrovoice 644 microphone. Vocalizations were analyzed with a Kay 6061B Sona-Graph.

Data on natural, aggressive interactions at the two feeders were also obtained in the same winter and dominance hierarchies were determined. A bird was considered to be dominant over another if it won an encounter or if one bird arrived after another but was the first to feed.

The behavior of chickadees was changed markedly by the mirror. When the mirror was absent a bird typically landed on the perch, entered the feeder and took a seed. When the mirror was present a bird usually landed and hopped from perch to perch several times and sometimes left without obtaining a seed. The experimental results for D7 feeder are shown

Table 2
Results of Mirror Experiments at F9 Feeder

Individuals[a]		No. visits in which seeds were taken				No. seeds/visit mirror[b]	No. visits when threats given to mirror
		baseline	mirror	baseline	foil		
COAY	♂	8	0	6	1	0 (5)	—
BOAW	♂	12	3	16	4	0.17 (18)	2
AOYB	♂	3	1	0	0	0.25 (4)	—
WPAO	♂	4	2	1	7	0.5 (4)	—
RYAO	♂	5	0	10	10	0 (2)	—
ROBA	♂	12	8	12	16	0.53 (15)	3
BRAO	♂	11	8	6	14	0.42 (19)	2
CBAO[c]		6	6	0	3	0.83 (7)	4
TOAT	♂	1	0	7	7	0 (2)	—
BACO	♀	0	0	7	6	0.15 (13)	—
RTAO	♂	7	0	5	3	0 (4)	—
AWYO	♂	1	0	8	2	0 (4)	—
AOSP	♂	8	2	1	1	0.25 (8)	—
JTAO	♂	1	0	2	2	0 (2)	—
AYRO	♀	9	1	4	7	0.13 (7)	—
POYA	♂	7	1	10	16	1 (1)	—
ACYO	♀	2	2	7	14	0.67 (3)	—
PORA	♂	2	0	3	1	0 (1)	—
GOAS	♀	3	0	0	0	0 (4)	—
AOYW	♀	9	0	1	1	0 (1)	—
AOPY	♀	5	0	0	2	0 (6)	—
BBAO	♀	1	0	2	2	0 (6)	—
COAJ	♀	5	0	2	8	0 (4)	—
ARCO	♀	3	0	0	0	0 (4)	—

[a] Listed in order of dominance.
[b] Total number of visits is in parentheses.
[c] Sex unknown.

in Table 1, for F9 in Table 2. The number of visits when seeds were taken with the mirror present was significantly lower as compared to the baseline at both feeders ($P < 0.001$ for F9, $P < 0.005$ for D7, Wilcoxon test, one-tailed). When the baseline was compared with the foil there was a significant difference ($P < 0.05$) for D7 but not for F9 ($P > 0.05$). When the number of seeds taken with the mirror present was compared directly to the number of seeds taken when the foil was present the difference was significant at both feeders ($P < 0.005$). The birds tended to take fewer seeds when either mirror or foil was present, but feeding was depressed more by the mirror.

In some cases threats, consisting of "gargles" and gapes, were directed at the mirror. Seven individuals (six males, one sex unknown) threatened the mirror; all were in the top half of their dominance hierarchy (Tables 1 and 2). "Gargles" vary in their syllabic composition, but the "gargles" at the mirror were not different from those typically given by that individual in natural encounters.

We also tested the hypothesis that dominant birds would take more seeds per visit with

the mirror than more subordinate birds. This hypothesis was not supported ($P > 0.05$, Kendall's tau).

The way in which a chickadee responds to its reflection depends in part on its past experiences in agonistic encounters and is reflected in its dominance rank. Birds that were more successful in winning contests were more likely to threaten the mirror, although threats were not confined to the most dominant birds as some males of mid-rank threatened the mirror. Even dominants tended to take fewer seeds when confronted with a mirror, indicating that they were somewhat intimidated.

A number of experiments with birds have employed models (e.g., Lack, Life of the Robin, Penguin Books, London, England, 1953; Dilger, Auk 73:313–353, 1956). A model is an unchanging stimulus, while a mirror reflects the animal's behavior exactly, except for vocalizations. Thus, a dominant bird sees one responding like a dominant, a subordinate sees one that acts like a subordinate. For birds with visual individual recognition the image would be a stranger. Mirror experiments are often difficult to interpret (Smith, The Behavior of Communicating: An Ethological Approach, Harvard Univ. Press, Cambridge, Mass., 1977), but they do show what an animal will do when confronted with an animal that looks and acts like itself. However, the image does not act like a copy because vocalizations are not returned, and this may be a very important difference for a species such as the chickadee which uses vocalizations frequently in agonistic encounters. However, our data show that chickadees will threaten a visual stimulus that is not accompanied by a vocal component.

We thank C. M. Weise for supplying data on the color-banded birds. Publ. No. 31 of the University of Wisconsin—Milwaukee Field Station. Supported by NSF grant BNS 7724932 to Ficken.—Ellen J. Censky and Millicent S. Ficken, *Dept. Zoology, Univ. Wisconsin–Milwaukee, Milwaukee, Wisconsin 53201.* (Present address EJC: *Section of Herpetology, Carnegie Museum, Pittsburg, Pennsylvania 15213.*) *Accepted 1 March 1982.*

Wilson Bull., 94(4), 1982, pp. 593–594

Tool use by Green Jays.—Tool use by birds has usually been defined as the manipulation of inanimate objects so as to extend the physical capabilities of the bird (Morse, Behavioral Mechanisms in Ecology, Harvard Univ. Press, Cambridge, Massachusetts, 1980). Corvids that use tools include the New Caledonian Crow (*Corvus moneduloides*) (Orenstein, Auk 89: 674–676, 1972), and laboratory-reared Blue Jays (*Cyanocitta cristata*) (Jones and Kamil, Science 180:1076–1078, 1973). Here I report tool use in the Green Jay (*Cyanocorax yncas*).

While studying this species at the Santa Ana National Wildlife Refuge near Alamo, Texas, I saw use of "tools" by a family of adult and juvenile Green Jays on 6 June 1981. I first observed an adult Green Jay (sex unknown) on the ground pick up a small twig in its beak and fly to a branch of a dead tree approximately 4 m above the ground. The bird inserted the twig under a piece of bark and moved it back and forth for approximately 5 sec. The jay then withdrew the twig, placed it under its feet, and proceeded to consume an insect that was attached to the twig. The bird then reinserted the twig under the bark and repeated the sequence of events four consecutive times, lasting about 2 min. The jay dropped the twig and flew a short distance to another tree. A few minutes later, the same adult flew back to the branch with another short twig in its beak and again inserted it under the bark. This time, however, the bird pried off a piece of bark, dropped the twig, and consumed the exposed insects. Whether the jay intentionally used the twig as a lever in this instance is unknown, since this behavior was not observed again.

A juvenile Green Jay attempted to use twigs to capture insects in a similar manner. One

of the apparent offspring (which had been seen begging for food earlier) of the previously mentioned adult jay picked up a twig and flew to the same branch on which the adult had been feeding. The juvenile inserted the twig several times under pieces of bark and removed it each time but did not capture any prey item. The total time spent attempting to feed in this manner was about 45 sec. The bird then dropped the twig, flew to the ground, picked up another twig, flew back to the same branch and tried again. After three unsuccessful attempts lasting about 2 min, the bird dropped the twig and flew to another tree. Due to the inaccessibility of the branch on which the jays were feeding, the types of insects being consumed were unknown.

To my knowledge, this is the first report of apparent tool use by wild jays. Of 14 individuals for which feeding data were collected, only these two birds were observed using tools and approximately 5% of the feeding observations for them involved tool use.

Acknowledgments.—I wish to thank J. Faaborg, R. Orenstein, and R. Raitt for comments on various drafts of this manuscript. R. Rauch and his staff at Santa Ana National Wildlife Refuge, especially R. Schumacher, were very helpful during my stay. The Frank M. Chapman Memorial Fund of the American Museum of Natural History provided support for this research.—DOUGLAS C. GAYOU, *204 Tucker Hall, Div. Biological Sciences, Univ. Missouri–Columbia, Columbia, Missouri 65211.* *Accepted 5 Apr. 1982.*

Wilson Bull., 94(4), 1982, pp. 594–595

A flight-song display of White-throated Manakin.—The White-throated Manakin (*Corapipo gutturalis*) is known in northeastern South America from the Guianas, Venezuela, and northern Brazil (de Schauensee, The Species of Birds of South America, Livingston, Wynnewood, Pennsylvania, 1966). The species favors hilly forest in Venezuela, between 250 and 1100 m elevation (de Schauensee et al., A Guide to the Birds of Venezuela, Princeton Univ. Press, Princeton, New Jersey, 1978). In Suriname the species is known from Brownsberg and Nassau Gebergte (Mees, Zool. Mededelingen 48:55–67, 1974). I have found White-throated Manakins fairly common at Brownsberg above 200 m from January–April and in November. It is a small, unobtrusive bird, foraging arboreally in small groups or among mixed flocks of honeycreepers and tanagers. The White-throated Manakin's presence is best betrayed by its foraging call, a high-pitched *SEE·seee* or *SEE·seee·ee·e*, uttered by both sexes.

Davis (Ibis 91:146–147, 1949) described White-throated Manakin displays from Guyana. The displays he observed involved a group of 6–12 birds of both sexes. At first, males displayed from tree branches between about 3–15 m above the ground, frequently chasing one another. Several times a male crouched with his bill pointing straight up, displaying the white throat. When a female flew down to a fallen tree trunk she was joined by a male and copulation took place without further display. Later, a female came to the log where she was joined by a male who crouched with wings fully spread horizontally and approached her with a slow and labored undulating crawl. The male's posture revealed the white wing bar at the base of the primaries. This display was interrupted by another intruding male. No calls were uttered by any of the birds present throughout the chases and displays. No further displays were noted at this spot later the same day or the next morning.

On 15 November 1979 M. Weinberger and I witnessed a male White-throated Manakin engaged in flight song display at Brownsberg. The display was remarkably like that given by male Common Yellowthroats (*Geothlypis trichas*) except that it took place above forest canopy rather than over dense, low cover.

Our observation was made 50 m beyond the driveable portion of the Mazaroni Val Trail, at 480 m elevation, where tree falls had created a semi-open clearing within the forest. Several trees 30–35 m in height stood isolated above a 5 m high jumble of secondary growth. As we passed this spot at 15:00 our attention was attracted by a series of high-pitched, insect-like notes from above. We saw a male White-throated Manakin fly up from the crown of one of the isolated trees. It flew in a shallow arc above the canopy, its white throat puffed-out, wings beating furiously, as it delivered its call in mid-air, then dove into the crown of a tree 12–15 m distant at the edge of the clearing, terminating the display with a wing snap. A tape-recording of the flight song, of insufficient quality to allow production of a sonogram, is on file at the Cornell University Laboratory of Ornithology sound library. A phonetic description is as follows: a 9-sec series of eight high-pitched notes starting at slightly above 7 kHz rising to about 8 kHz with increasing intensity, terminating with a snap, e.g., *seeee·seeee·seeee·seeee·seeee·seeee·seeee·seeee-snap*. The song flight was delivered back and forth between the same two trees four times in 5 min. The male then disappeared for 15 min, then displayed once again, then departed. About 5 min later, a male reappeared chasing a female through the forest about 10 m overhead with short, agitated bursts of flight. During the chase, one of the birds uttered a sharp *seee·ee*. I revisited this spot in November 1980 and February 1981 and observed no further displays.

Snow (pp. 553–561 *in* Proc. XIII Inter. Ornithol. Congr., Ithaca, New York, 1963) mentions display flights in his synopsis of manakin displays. However, his summary does not indicate that any of the species known to possess display flights performed them high above their normal habitat. The unique flight-song display above the forest canopy here described for the White-throated Manakin is also exhibited by another closely allied, allopatric member of *Corapipo*. John Rowlett (pers. comm.), of Austin, Texas, was birding in elfin forest habitat above Cerro Azul, Panama, during February 1978 when he witnessed several male white-ruffed Manakins (*C. leucorrhoa*) in flight song display. Up to three males were involved at a given moment. Each bird flew straight up to about 15 m above the canopy, hovered briefly, then plummeted back into the forest. A series of high-pitched *seee* notes was delivered in flight, but Rowlett was uncertain if these were uttered as the birds were climbing or dropping. Also, the terminal wing snap was not detected.

I am indebted to Marc Weinberger for his field assistance, J. Rowlett for use of his field notes, J. DiCostanzo and M. Foster for providing needed references, Guy Tudor for reviewing the manuscript, and STINASU (Stichting Natuurbehoud Suriname) for arrangements during my Suriname visits.—Thomas H. Davis, *9446 85 Road, Woodhaven, New York, New York 11421.* *Accepted 20 Feb. 1982.*

Wilson Bull., 94(4), 1982, pp. 595–598

Notes on the agonistic behavior of Common Murres.—Common Murres (*Uria aalge*) nest colonially and in fact breed at greater densities than almost any other bird species (see Tuck, The Murres, Can. Wildl. Serv. Monogr. Ser. 1, 1961). However, once away from breeding sites they occur singly or in loose aggregations (Williams, M.Sc. thesis, Univ. Sheffield, Sheffield, England, 1972). The social situation during the non-breeding season is quite different from that during breeding, where extreme crowding is possible through the inhibition of intense aggression and escape tendencies. The problems presented by this highly stressful situation (breeding conditions) have been well defined by Birkhead (J. Anim. Ecol. 46:751–764, 1977).

Williams (1972) appraised the forms and origins of Common Murre behaviors, while Birk-

head (Anim. Behav. 26:321–331, 1978) analyzed quantitatively the 14 displays described for this species. The present study was carried out to increase our knowledge of murre agonistic behaviors. The basic terminology used and the behaviors observed follow the scheme of Birkhead (1978). Agonistic behaviors are considered to be those that increase or decrease interaction distance from overt attack to escape (Scott, Am. Zool. 6:683–701, 1966; Manning, An Introduction to Animal Behaviour, 2nd ed., Addison-Wesley Publ. Co. Don Mills, Ontario, 1972).

Observations were made at various distances from several breeding ledges in a new and rapidly expanding colony on Gull Island, Witless Bay, Newfoundland, in 1977 and 1978 (Mahoney, M.Sc. thesis, Memorial Univ., St. John's, Newfoundland, 1979). Sites were chosen to minimize disturbance. The oblique nature of the slopes above the ledges and the presence of rock outcroppings allowed us to approach within 10–15 m of the birds without causing alarm, although we usually remained 50 m away. Observations were made using 7 × 35 binoculars and a 15–60× spotting scope.

Common Murres breed so densely that aggressive confrontations occur frequently. Three levels of intensity were recognizable: level 1—"jabbing," directed at the opponent's bill without contact; level 2—similar to level 1, but contact was made and the target included the neck and head; level 3—"jabbing" with half-open beaks, leading to locked bills, twisting heads, and beating with the wings. Only 30 level 3 encounters were recorded in two seasons of fieldwork, which is far fewer than Birkhead's (1978) 200 in four seasons. It indicates that intense aggression is less frequent on Gull Island than on Skomer, with the difference probably being due to colony size and lay-out.

Jabbing was the most frequent expression of overt aggression, with one bird thrusting its bill towards another, sometimes making contact and sometimes in a ritualized form. In the initial stages of confrontation jabbing was directed only at the head and bill of the opponent, but during later stages intensity of jabs increased.

Level 2 was usually preceded by "threat display," and normally occurred with the birds about 0.3 m apart and facing the cliff. The birds maintained a distance in which actual physical contact could occur. Once a level 2 encounter intensified to level 3 the "critical distance" was broken down and fighting occurred. The critical distance was well defined; threat posturing between two birds greater than 0.5 m apart occurred in only 3 of 200 (1.5%) threat displays observed. In 76 (38%) of these, threat was accompanied by a low "gargling" call. These threat displays developed to level 3 intensity in only four (2%) cases, or 13% of the total level 3 encounters observed (N = 30). Level 3 encounters seldom exceeded 2 min, but one fight lasted 17 min, with both combatants becoming bloodied. In long encounters the birds became fatigued and often rested with beaks and necks entwined. As soon as one bird gripped its opponent by the lack of the neck struggling ceased. The low frequency of violent confrontations indicates strong inhibitions against them. Such inhibitions, coupled with the gradations in the intensity of encounters, essentially perform the function of aggression, namely protection of site, mate, and self.

During level 3 encounters antagonists seemingly lost all inhibitions towards the crossing of territories, and scrambled about the ledge. Incubating birds never responded to these intrusions even though they were often struck by the wings of the fighting birds, and birds not incubating were seen to retaliate only twice (6.6% of the occasions). This absence of retaliation by non-combatants presumably prevented damage to chicks and eggs. On the other hand, trespassing birds shuffling among incubating birds were normally attacked (level 1) by territory owners. The trespasser rarely retaliated and usually fled (see Williams 1972). Challenges invariably ended with head-shaking (Williams 1972; this study); the head was lowered as shaking occurred until eventually it touched the breast or shoulder at which point preening commenced. Thus, head-shaking connects the alert challenge posture of potential

aggression with an appeasement gesture. In contrast to Birkhead (1978), it was noted here and in Williams' (1972) study that head-shaking occurred before any winner or loser in an encounter could be determined. Ainley (Behaviour 50:16–51, 1974) noted a similar movement in Adélie Penguins (*Pygoscelis adeliae*) and suggested that it may be concerned with the removal of water, salt gland fluids, and other extraneous materials from the nostrils. This behavior also occurred frequently in non-agonistic situations and was usually associated with gape-distension similar to the "jaw-stretch" in ducks (McKinney, Behaviour 25:120–220, 1965) and "yawn" in penguins (Ainley 1974). In the latter context it was a comfort movement. Body maintenance behaviors are likely candidates for ritualization as they contain no threat components. Gape-distension, accompanied by loud calls, was also observed in the female during copulation.

Both Birkhead (1978) and Williams (1972) commented on seasonal aspects of murre aggressive behavior. On 63 occasions, unprovoked, random attacks (level 1), followed immediately by appeasement gestures, were observed during incubation and fledging. Fewer than 10 such behaviors were noted in the pre-laying period, and none when the birds first returned to the ledges. The latter is in direct contrast to the situation reported by Birkhead (1978).

Aggressive encounters were usually associated with territory defense or exhibited by the mate in cases of attempted rape. In 42 such attempts, the female resisted while her mate attacked the rapist, the latter never retaliating. On only two occasions was intra-pair aggression observed, both of which involved copulation, with the female jabbing vigorously at the male. Birkhead (1978) also noted a low level of intra-pair aggression on Skomer.

On Gull Island aggressive jabs frequently and abruptly gave way to appeasement. Obviously, if mechanisms to mitigate aggression had not evolved, dense coloniality could never have become successful. Birkhead (1978) separated murre appeasement into passive displays which prevent aggression, and active displays which terminate it, and noted that certain displays in different contexts function in either capacity. This latter point is well illustrated in the case of "side-preening," the most frequent appeasement behavior seen on Gull Island. It was performed upon return of a bird to its site, at the end of fights in the middle of level 2 encounters, and as an ending to threat-only confrontations. Birkhead's (1978) contention, conflicting with that of Williams (1972), that no directional component is involved in this behavior, was supported by our observations.

The "preening" during side-preening was token in nature, and emphasized the ritualization of the posture. During 340 observed returns-to-site, all of which could have resulted in aggression, 311 (91%) birds side-preened immediately or just after "bill-arring" with their mate. In 167 (54%) of returns that included appeasement, neighbors adopted a challenge or threat posture, and in 42 (25%) they jabbed the newly arrived individual. In all but seven of the latter, aggression terminated with the appeasement posture. Thus, in only 2% of the cases did post-appeasement aggression occur. Birds returning to an unoccupied site (mate absent) always side-preened, indicating that non-mate conspecifics may solicit this response. In the 9% of returns-to-site where side-preening was not recorded, all birds performed bill-arring.

"Stretch-away" and "turn-away" appeasement occurred after an aggressive encounter involving the bird showing appeasement, or in response to a nearby high level encounter, and in response to the movement of nearby birds. Stretch-away was performed only by incubating birds and was mainly a passive gesture (88% [76 of 86 observations]). During active appeasement the neck extension was sometimes maintained even while the bird was jabbed by its opponent.

Turn-away occurred infrequently as passive appeasement, and in 121 of 127 observations (95%) it occurred immediately after level 2 or level 3 confrontation. It followed threat encounters in only 3% of cases. In five level 2 encounters, where turn-away was used to terminate aggression, the initial jabs were responses to the stretch-away elicited by the move-

ment of a nearby bird. Paradoxically, one appeasement gesture elicited aggression and thereby necessitated a different appeasement display. These observations underline the high tension inherent in murre breeding colonies and demonstrate how sudden movements often elicit aggression.

A passive appeasement behavior, the "post-landing display," was observed in 324 of 360 instances (90%) where birds alighted within 1 m of conspecifics or where they followed landing with movement through the colony. Murres landing and remaining on the periphery of a group seldom performed post-landing display, which is in contrast to Williams' (1972) observations. Birkhead (1978) also noted that birds were more likely to perform it in the proximity of other birds. This display is probably a combination of recovery after landing and preparation for attack, defense or fleeing (see van Tets, Ornithol. Monogr. No. 2, 1965). After landing, a murre must usually cross several territories in order to reach its egg or mate. On Gull Island, if the bird could walk past a group at a distance of 2 m or more no posture was assumed. However, if it had to walk by at less than this distance it usually (78% [161 to 207 observations]) adopted "ritualized-walking I," which included head-down and wings-up-and-back components. In 35% of observations the latter component was abandoned. This indicates that head-down is the most essential component of the display, and certainly, if, as Birkhead (1978) suggests, the wing component draws attention to the moving bird, then it may be that the post-land display, which preceded ritualized-walking I, accomplished this already.

When a murre had to move through a nesting group it adopted "ritualized-walking II," which was practically identical to post-landing display, except that in 23 of 63 instances (37%) the wings-up-and-back component was lacking. This usually occurred where the latter aspect might have elicited aggression from birds struck by the wings. The appeasement function of this display was demonstrated in two ways. First, of 15 situations where birds did not adopt this posture, 14 (93%) resulted in threats or level 2 encounters. Second, in eight (57%) of these situations, birds once threatened or attacked, stretched the neck high and positioned the bill almost vertically. If the attacker was to one side or behind them, the birds hurried out of range; if their path was blocked by the aggressor, then they stopped and usually accepted several jabs without retaliation. Aggression was always alleviated by exaggeration of the basic posture and level 3 encounters never developed.

We observed no behaviors not also recorded by Birkhead (1978). A possible exception was the exaggerated form of the ritualized-walking II display, which bore a strong resemblance to Birkhead's (D. Phil. thesis, Oxford Univ., Oxford, England, 1976) "head-vertical" posture. He interpreted this display as one of advertising performed almost exclusively by non-territorial (non-mated) males. The posture illustrated by Birkhead (1976) is apparently identical to the one observed on Gull Island and it may be that the posture functions in both contexts—male advertising and active appeasement—both being situations requiring conspicuous non-aggressive intent.

This work was conducted under a post-graduate fellowship awarded to S. Mahoney and a grant (A3500) to W. Threlfall, both from the Natural Science and Engineering Research Council of Canada.—Shane P. Mahoney, *Newfoundland Wildlife Div., Bldg. 810, Pleasantville, St. John's, Newfoundland A1C 5T7, Canada* and William Threlfall, *Dept. Biology, Memorial Univ., St. John's, Newfoundland A1B 3X9, Canada.* *Accepted 15 Feb. 1982.*

Wilson Bull., 94(4), 1982, pp. 599–602

Records of Redhead × Canvasback hybrids.—Because of similarities in habitat use, courtship display, and appearance, Canvasbacks (*Aythya valisineria*) and Redheads (*A. americana*) have long been suspected to hybridize in nature (Hochbaum, The Canvasback on a Prairie Marsh, Stackpole Co., Harrisburg, Pennsylvania, 1944; Weller, Auk 84:544–559, 1967). This notion has been strengthened by observation of interspecific courtship in the wild (Hochbaum 1944:40; Weller 1967:557; Timken, Auk 84:588, 1967), and by record of a few captive hybrids (Gray, Bird Hybrids, Commonwealth Agric. Bur., Bucks, England, 1958). Hybridization is of particular interest because the Canvasback is often principal host for Redhead nest parasitism (Weller, Ecol. Monogr. 29:333–365, 1959; Sugden, J. Field Ornithol. 51:361–364, 1980), a relationship requiring special adaptation with regards to Redhead sexual imprinting to maintain species isolation (Mattson and Evans, Can. J. Zool. 52: 421–427, 1974). A review of the literature has indicated that only a single suspected wild hybrid has been reported (McIlhenny, Bird-Banding 8:119, 1937).

While trapping Canvasbacks on the Potomac River near Dahlgren, King George Co., Virginia, I captured two suspected Redhead × Canvasback adult male hybrids that I later banded and released. The first hybrid was caught on 8 January 1980, and the second on 5 January 1982. Weight and wing chord measurements of the hybrid birds agreed closely with measurements of adult male Canvasbacks captured with them (Table 1). Both hybrids resembled male Canvasbacks in body and wing plumage, but were intermediate between Canvasback and Redhead in the structure and coloration of the head, neck, and bill (Fig. 1). Both bill and neck appeared shorter and the bill and crown were more rounded, i.e., less wedge-shaped than in the Canvasback. Head and neck plumage of both hybrids was chestnut-red, like that of the Redhead. The head lacked the dark wash and particularly the black face and crown of the Canvasback. The bill was marked like that of the Redhead, having a black tip, a white subterminal band, and pale-blue coloration extending well past the nares to near the base of the bill. The eye of both hybrids was yellow-orange, intermediate between the yellow eye of the Redhead drake and the scarlet-red eye of the male Canvasback. This may not have been the true eye color of the hybrids, however, for I have often observed the eyes of male Canvasbacks turn yellow as a result of capture stress. The scapular plumage of the hybrid birds was near-white but slightly darker than is characteristic of the Canvasback.

A survey of Canvasback and Redhead banders over the past decade revealed the capture

Table 1

Weight and Wing Chord Measurements of Redhead × Canvasback Hybrids and Canvasbacks Captured on the Potomac River

Date	Specimen[a]	Weight (g)	Wing chord (mm)
8 Jan. 1980	Redhead × Canvasback	1360	239
	Canvasback (N = 45)	1353 ± 13[b]	239.4 ± 0.4
5 Jan. 1982	Redhead × Canvasback	1430	240
	Canvasback (N = 16)	1357 ± 13	240.3 ± 0.7

[a] All birds are adult males.
[b] Mean ± standard error.

FIG. 1. Adult male Redhead × Canvasback hybrid captured on the Potomac River near Dahlgren, Virginia. 8 January 1980.

of four additional hybrids (Table 2): all were males, two of which were placed in the National Museum of Natural History in Washington, D.C. Three of the birds were captured from Canvasback flocks, and a single hybrid, captured by R. Ryan, was obtained from a Redhead flock.

I visited the National Museum to compare the hybrid study skins with the hybrids from the Potomac River. I also obtained photos of Ryan's hybrid and a description of Munro's 1972 capture (R. Munro, pers. comm.). Comparison of all six hybrids showed that five of the birds, all captured from Canvasback flocks, resembled the Potomac River hybrids as earlier described. These five hybrids resembled the one wild male and one captive-propagated male hybrid briefly described by McIlhenny (1937:119) and Weller (Wilson Bull. 69:32, 1957), respectively. Ryan's hybrid, the only hybrid captured from a Redhead flock, appeared to be structurally similar to the other hybrids, but had body plumage that matched that of the Redhead and head and bill coloration that was more Canvasback-like. The bill of this bird was black except for faint blue patches near its base. Following an earlier study of *Aythya*

TABLE 2

ADDITIONAL CAPTURES OF REDHEAD × CANVASBACK HYBRIDS FROM A SURVEY OF CANVASBACK BANDERS 1972–1982

Bander	Date	Location	Description
Robert Munro	Dec. 1972	Eastern Neck National Wildlife Refuge, Rock Hall, Maryland	adult male; escaped unbanded
Robert Munro	6 Feb. 1974	Gibson Island, Maryland	adult male; collected[a]
Richard Ryan	14 Feb. 1976	Seneca Lake near Geneva, New York	immature male; 1380 g, released
Jerome Serie	11 Nov. 1976	Pool 8, Mississippi River near Stoddard, Wisconsin	adult male; 1590 g, collected[a]

[a] Study skin placed in National Museum of Natural History, Washington, D.C.

hybrids (Gillham et al., Wildfowl Trust Ann. Rpt. 17:49–65, 1966), these hybrids could be broadly categorized as "Canvasback-type" and "Redhead-type" hybrids, respectively. Other hybrid types may also occur, particularly since hybrid fertility has been documented (Weller 1957:33) and backcrossing is likely to occur.

I also compared study skins of hybrids with those of *A. valisineria*, *A. americana*, and the palearctic Common Pochard (*A. ferina*), a species known to resemble Redhead × Canvasback hybrids (Weller 1957:32; Delacour, The Waterfowl of the World, Country Life Ltd., London, England, 1959:61). My observations confirmed the close resemblance particularly in head and bill structure between hybrid and *A. ferina* specimens, although the latter were clearly smaller birds. The scapular plumage of *A. ferina* specimens was found to be particularly close to that of the "Canvasback-type" hybrids, but contrasted sharply in color with the "Redhead-type" hybrid.

Measurements of museum study skins (Table 3) show that Canvasbacks have a significantly larger culmen ($t = 20.0$, df = 26, $P < 0.01$) and wing chord ($t = 2.27$, df = 15, $P < 0.05$) than Redheads; Common Pochards have a culmen length similar to Redheads ($t' = 1.34$, df = 25, $P > 0.05$) but exhibit a significantly shorter wing chord ($t = 12.8$, df = 17, $P < 0.01$). Live weights of adult males confirm the size differences in these three species: Canvasbacks averaged 1326 g (N = 247) during January 1978 on the Chesapeake Bay (Nichols and Haramis, Condor 82:412, 1980), Redheads averaged 1226 g (N = 90) during January in New York State (1960 and 1971 data combined from Ryan, J. Wildl. Manage. 36:761, 1972), and the Common Pochard averaged 849 g (N = 119) from December to February in the Camargue, France (Bauer and Glutz von Blotzheim, Handbuch der Vögel Mitteleuropas, Frankfurt am M., W. Germany, Vol. 3, 1969). Measurements from hybrid birds show them to have a wing chord similar to the Canvasback, culmen length intermediate between Canvasback and Redhead (Tables 1 and 3), and weight in the upper range of the Canvasback (Tables 1 and 2).

Evidence from the current Canvasback banding program on the Chesapeake Bay suggests that Redhead × Canvasback hybrids are rare. An examination of over 13,000 Canvasbacks yielded only two hybrids. Other hybrids probably occurred, but were less distinctive and went unrecognized. Female hybrids are especially hard to detect (cf. Gillham et al. 1966).

Table 3

Measurements of Male Study Skins at NMNH[a] and Live Redhead × Canvasback Hybrids Captured on the Potomac River

Specimen	Culmen (mm)	Wing chord (mm)
Redhead × Canvasback hybrids		
I.D. No. 567521 (Munro, 6 Feb. 1974)	54.5	237
I.D. No. 573675 (Serie, 1 Nov. 1976)	56.4	240
Potomac hybrids (8 Jan. 1980)	58.0[b]	239
(5 Jan. 1982)	58.2	240
Typical specimens[c]		
Canvasback[d]	61.4 ± 0.5[e]	239.3 ± 1.1
	N = 16	N = 7
Redhead[f]	48.4 ± 0.4	235.7 ± 1.1
	N = 12	N = 10
Common Pochard[g]	47.4 ± 0.7	212.8 ± 1.4
	N = 15	N = 9

[a] National Museum of Natural History, Washington, D.C.
[b] Estimated from photographs.
[c] Culmen measurements taken from adult and full-grown juvenile specimens; wing chords taken from adult males only.
[d] Specimens are from Maryland (8), Texas (3), Delaware (2), North Dakota (1), Louisiana (1), and Mississippi (1).
[e] Mean ± standard error.
[f] Specimens are from North Carolina (3), Texas (3), North Dakota (2), Pennsylvania (1), California (1), Oregon (1), and Utah (1).
[g] Specimens are from Europe (8), Egypt (2), Alaska (3), India (1), and Turkey (1).

Acknowledgments.—I thank R. Browning and M. Foster of the National Museum, and E. Derleth, D. McAuley, and C. Samuel for technical assistance. My appreciation is extended to R. Ryan for slides of his hybrid bird, and M. G. Anderson, T. J. Dwyer, and M. W. Weller for their review of the manuscript.—G. M. Haramis, *U.S. Fish and Wildlife Service, Patuxent Wildlife Research Center, Laurel, Maryland 20708. Accepted 1 Apr. 1982.*

Wilson Bull., 94(4), 1982, pp. 602–603

High mortality of Cedar Waxwings associated with highway plantings.—Highway mortality in birds is a commonly reported phenomenon, but few studies identify specific factors affecting such mortality. On 8 March 1981 we observed a number of Cedar Waxwings (*Bombycilla cedrorum*) being hit by cars at several areas on the Texas Highway 6 bypass, a limited access highway, near Bryan, Brazos Co., Texas. At each area the birds were feeding on the fruit of silverberry (*Eleagnus pungens*) planted in the median of the four-lane highway. The shrubs were 1.5–2 m in height and were 3.5 m from the paved shoulder of the highway. The Texas Department of Highways planted *E. pungens* along the bypass in 1974. As cars passed, feeding flocks of waxwings flew up, crossing the highway, only to return immediately to the shrubs with several birds being hit with each pass of the flock.

At three such areas along Highway 6, totaling 275 m of plantings over a 3 km section of highway, we counted a total of 298 dead Cedar Waxwings between 8 March and 5 April

1981. This total is based on initial counts at these areas on 8, 11, 12, and 16 March and recovery of all dead birds on 22 March and after. The total mortality was probably higher than 298 due to loss of birds between counts and recovery periods as suggested by Stewart (Wilson Bull. 85:203–204, 1973). The largest single count was 133 birds on 11 March at an area with 25 individual shrubs planted over a distance of 100 m. We also found two Northern Mockingbirds (*Mimus polyglottos*) and one Red-winged Blackbird (*Agelaius phoeniceus*) at that locality.

All dead birds were associated with median plantings; we found no birds at plantings of *E. pungens* along entrance ramps or on either side of the highway. Although no extensive effort was made to monitor other areas with median plantings of *E. pungens* along Highway 6 bypass, no large kills were apparent at other areas. This could be because the flock or flocks concentrated on the first source of *E. pungens* they encountered and did not seek other sources until the first supply of berries was exhausted. At these areas berries remained available throughout the study period. The nearest sets of other median plantings of *E. pungens* were 5.1 km to the north and 7.2 km to the south. We assume the original flock continued to feed in the same area over a 4-week period because the size of the flock decreased noticeably, to a low near 10 individuals, as birds continued to be killed.

Although many studies document the impact on wildlife of cover reduction near highways (see Leedy, Fed. Hwy. Admin. Rept. No. FH WA-RD-76-4, 1975), no studies to our knowledge report the potential adverse effect of highway plantings on animal populations. The factors which led to the high kill of waxwings in this case were the presence of the shrub plantings in the median so close to the edge of a high speed (55 mph) highway; the heavy crop of fruits attractive to the birds, especially during the winter season when they are present in the area in peak numbers; and the flushing and flight behavior of the waxwings, which makes them particularly vulnerable. In view of the above described waxwing mortality, narrow highway median strips should not be planted in shrubs or trees providing fruits or other sources of food attractive to flocks of migratory and wintering birds.

We thank the Bryan office of the Texas Department of Highways for providing information and K. A. Arnold for his comments on the manuscript.—Robert C. Dowler, *Dept. Wildlife and Fisheries Sciences, Texas A&M Univ., College Station, Texas 77843*; and Gustav A. Swanson, *Dept. Fishery and Wildlife Biology, Colorado State Univ., Fort Collins, Colorado 80523.* (Present address RCD: *Dept. Biological Sciences, Fordham Univ., Bronx, New York 10458.*) *Accepted 20 Feb. 1982.*

Wilson Bull., 94(4), 1982, pp. 604–611

ORNITHOLOGICAL LITERATURE

Voices of New World Nightbirds. Record # ARA–6. Produced and narrated by John William Hardy. Principal recordist, Ben B. Coffey, Jr. Produced in the Bioacoustical Laboratory of the Florida State Museum. ARA Records, 1615 N.W. 14th Ave., Gainesville, Florida 32611, 1980. One LP record in jacket. $7.00.—For cogent commentary and background on this series see the reviews by Stuart Keith (Wilson Bull. 88:525–526, 1976; 90: 148–150, 1978).

Presumably I was asked to review this effort because my wife and I are among the comparatively few who have engaged in the "tedious work . . . at what for most of us are 'unnatural' times for concentrated, accurate endeavor," involving "considerable danger . . . and immense patience" in efforts to extend our knowledge beyond "mysterious . . . evidence that some birds out there are doing something" (jacket text). Our efforts (for part see Living Bird 10:170–184, 1971) involved only Chuck-will's-widows (*Caprimulgus carolinensis*) and Whip-poor-wills (*C. vociferus*) in tame Kansas. We rarely found the work tedious, however, and for us the dangers were limited to inconveniencing the odd copperhead and, once, nearly netting a deputy sheriff on his way to an accident. But we did learn how difficult the work can be and I am awestruck by the amount that underlies this pioneer compilation (30+ contributions by Coffey, the rest by a long series of others, especially Paul Schwartz, George Reynard, Joe T. Marshall, Jr., and Hardy).

Therein appear vocalizations attributed, at least tentatively, to about 45 species of owls and 30 of caprimulgiforms. Hardy tells me that about 35 of these are presented here for the first time on a commercially available disc. Most, if not all, are basic territorial "songs" or epigamic vocalizations. Since these night birds communicate mainly by sound, probably all employ considerable vocabularies, as we found for the Kansas goatsuckers. Although vocalizations other than advertising song are now known for at least a few species, Hardy did not use these, probably because of space limitations.

Perhaps also for this reason, the record lacks the extensive spoken commentary with which Stuart Keith earlier took issue (at length notable for a discourse on succinctness). The record would have been enhanced by written commentary more extensive than the jacket will accommodate, but this will mainly concern those of us who are laypersons concerning the esoterica of nightbird systematics. Space, again, may have prevented identification of some of the fascinating sounds that appear as background.

Acoustical quality ranges from good to superb, perhaps depending somewhat upon distance. I was impressed by how many owls and goatsuckers sound much alike, respectively, and by how consistently the sound-alikes are allopatric. It is not far from this to the notions that quite a few of these sounds must be primitive for the groups, hence without systematic information content at the alpha level, and that few patterns suggest the shared derivation that would convey such information (*Caprimulgus carolinensis-C. rufus* may be one of these).

The first of two cuts given as "*Caprimulgus parvulus*" belongs to a population now regarded as a distinct species, *C. anthonyi* (Schwartz, Condor 70:223–227, 1978; Bock and Farrand, Am. Mus. Novit. 2703:25, 1980).

This record represents a heroic collective effort and, besides being of considerable value, provides very pleasant and often amusing listening. Hardy is again to be congratulated.—Robert M. Mengel.

The Molt of Scrub Jays and Blue Jays in Florida. By G. Thomas Bancroft and Glen E. Woolfenden. Ornithological Monographs No. 29, American Ornithologists' Union, Washington, D.C., 1982:vii + 51 pp., 15 text figs., 16 tables. $8.00 ($6.50 to AOU members).—

This monograph describes in detail the molt of Scrub Jays (*Aphelocoma coerulescens*) and Blue Jays (*Cyanocitta cristata*) resident at the Archbold Biological Station in central Florida. The thorough presentation of this information, in text and a series of tables and figures, is the crux of the publication. It seems likely, based on this publication, that these jays will now be used to exemplify the passerine molt pattern and as a basis for comparison within the passerines.

A series of short, to-the-point, comparative and analytical discussions are included. Comparison is made within each species between the molt of the different age/sex/breeding status classes. Published accounts of molt in other populations are used in a second intraspecific comparison. Finally, the two species are compared to each other. The authors attempt, with healthy restraint, to put molt differences into an ecological context. For example, a major difference between the species occurs in the first prebasic molt. Young Scrub Jays molt their head feathers gradually, earlier in the summer, while Blue Jays have a sudden capital tract molt late in the season. During nesting, the authors suggest, juvenal head feathering may reduce aggression. After territoriality ceases, an adult appearance may be best in terms of establishing a position in aggregations. The persistence of nesting and territoriality by Blue Jays for two months longer than Scrub Jays may be the reason for the delayed juvenal head molt in young Blue Jays.

The two species provide differing contributions to the publication. A great deal is known about Scrub Jays, in Florida and elsewhere. Very little is known about Blue Jays. These particular Scrub Jays have been under study by Woolfenden since 1969, and virtually all were banded, with age, sex, and breeding history known, at the beginning of the fieldwork for this paper. Few of the Blue Jays were already banded, and, amazingly, no other papers have detailed the molt or breeding biology of Blue Jays. In filling the molt part of this void, the inclusion of the Blue Jay is justified. However, analysis in this paper relies largely on data from the Scrub Jays.

The knowledge, for Scrub Jays, of individual breeding status and timing is critical, allowing a more detailed level of analysis than is the norm in molt studies. For example, Blue Jay and Scrub Jay molt as a whole seems to overlap with breeding. For Scrub Jays, the overlap can be more closely examined. It appears that most birds, including breeding males and helpers, initiate molt in May, regardless of the individual state of breeding, although breeding males may be molting at a slow rate while eggs are in the nest. The breeding females do delay molt until after their eggs hatch.

With this detailed view, additional discussion centers on molt and the breeding season. The species are appropriate for further questioning of this relationship, firstly because of the individual knowledge of breeding timing, and secondly because they are resident species in a moderate climate zone. Complicating stresses of migration and cold are not present.

After carefully estimating the energetic cost of molt, the authors reject the idea that molt and breeding are separated by energy restrictions. Molt is suggested to be not so expensive, at least not initially and not when protracted. Anyway, it is the foraging males and the helpers that appear to be expending the most energy, while it is the breeding female that delays her molt. The authors discuss other possible explanations, preferring the idea that a complete feather coat protects the female, restricted to the nest, from solar radiation. Males and helpers have less need for such protection because they can move about and use microhabitats. Other factors, such as water balance, may also be involved.

The terminology is dense at times, but the methods section, read carefully, will keep things straight. I would prefer precise definitions for such terms as "adult" and "yearling," or use of the strictly defined age codes used by bird-banders. Pertinent literature, including Russian publications, is thoroughly reviewed, although the absence of reference to a paper on Blue Jays in central Florida (Nicholson, Wilson Bull. 48:26–33, 1936) seems peculiar.

This monograph combines a wealth of detail with an interesting approach to the social and ecological contexts of molt. I strongly recommend it.—Peter F. Cannell.

Birds at Risk. A Comprehensive World-Survey of Threatened Species. By Ralph Whitlock. Moonraker Press, Wiltshire, United Kingdom (distributed in U.S. by Humanities Press, Atlantic Highlands, New Jersey), 1981:159 pp., numerous color paintings (by Matthew Hillier), color and black-and-white photos, and maps. $30.00.—Although this book purports to be a global survey of avian extinction and its causes, its author is plainly out of his depth when he ventures beyond the British Isles. The text wanders erratically among topics of varying relevance to the subject (such as eutrophication), repeating much of the material twice or three times in different chapters. The illustrations, though attractive, are poorly chosen; the abundant White-winged Dove (*Zenaida asiatica*), not mentioned in the text, is the subject of a full-page color photograph.

Poor organization, however, is a minor problem compared with the numerous inaccuracies in the text. Misspellings of Latin, vernacular, and place names abound. Nomenclature is often incorrect or out of date (*Siphonorhis* spp., for instance, are repeatedly called "nighthawks"). Taxonomic misstatements place *Diomedea irrorata* as a race of *D. exulans* (p. 49), *Rhipidura* in the Remizidae (p. 63), *Burhinus* as "a near relation of the bustards" (p. 123), icterids as "closely allied to the European Starling" (p. 145), and the Tuatara as a lizard (p. 24)! Other errors cover, for instance, distribution (the Ruby-throated Hummingbird [*Archilochus colubris*] is not found "in the western states of America and British Columbia" [p. 146]), status (the possibly extinct Paradise Parrot [*Psephotus pulcherrimus*] is hardly "reasonably safe" [p. 74]), and ecology (not only is the Nihoa Millerbird [*Acrocephalus kingi*] not a "reed-haunting species" [p. 53], Nihoa lacks reeds!).

The author appears unaware of much of the recent literature, including the revised edition of the IUCN Red Data Book volume on Aves. He has overlooked the rediscoveries of the Maui Akepa (*Loxops coccinea ochracea*) (p. 21), Maui Nukupu'u (*Hemignathus lucidus affinis*) (p. 22), Auckland Island Rail (*Rallus pectoralis muelleri*) (p. 27), Guadeloupe House Wren (*Troglodytes aedon guadeloupensis*) (p. 34), Giant Canada Goose (*Branta canadensis maxima*) (p. 39), Maui Parrotbill (*Pseudonestor xanthophrys*) (p. 52), and Night Parrot (*Geopsittacus occidentalis*) (p. 103); recent records of Madagascar Teal (*Anas bernieri*) (p. 73) and Western Tragopan (*Tragopan melanocephalus*) (p. 95); removal from endangered status of the Narcondam Hornbill (*Aceros narcondami*) (p. 61) and Tinian Monarch (*Monarcha takatsukasae*) (p. 65); and addition to the Red Book of the Tooth-billed Pigeon (*Didunculus strigirostris*) (p. 32).

The author's attempt to discuss extinction and its causes betrays a poor understanding of both biology and history. According to Whitlock, the disappearance of the Laysan Honeyeater (*Himatione sanguinea freethi*) "seems to have been [!] in some way associated with the introduction of rabbits" (p. 23); "Starlings are usually able to adapt themselves, and this species [*Aplonis corvina*] was a large and robust bird, so its disappearance seems strange" (p. 32); "The second extinct wader of the Pacific . . . is extinct only as far as Christmas Island is concerned" (p. 33); oceanic island birds "are inclined to adopt the form of birth control which consists of laying only one egg a year" (p. 47); "To maintain a stable population it needs only for a pair of birds to reproduce themselves before their decease. Most small birds do this in a single year, so their own survival into a second year is not important" (p. 143)!

These are only a few (and not necessarily the worst) of the errors and misconceptions in this slipshod work. Its publication smacks of exploitation, and should be condemned by

conservation-minded ornithologists working to bring the real facts before the public. It is most unfortunate that Whitlock's book has received the recommendation, proudly displayed on the dust jacket, of the World Wildlife Fund.—Ronald I. Orenstein.

Hawaiian Birdlife, 2nd edition. By Andrew J. Berger. The University Press of Hawaii, Honolulu, Hawaii, 1981:260 pp., 67 color plates, 137 black-and-white figs. $29.95.—This is an expanded and updated version of the standard work on the birds of the Hawaiian Islands. Like the first edition (1972) it differs from the most state bird books in giving not only species descriptions and distributions, but in emphasizing the ecological and historical effects of man's insensitive exploitation of Hawaii on its remarkable avifauna. The new edition shows that the islands still hold some ornithological surprises, such as the discovery in 1973 of a new passerine genus, *Melamprosops*. Additionally, a great deal has been learned in the past decade about the life histories of Hawaiian birds, and this has been incorporated into expanded species accounts. Unfortunately, too many people are still largely unknowing or uncaring about the devastating effects of habitat destruction and the introduction of exotic species on the native birds. Berger writes (p. 23) ". . . because of the destruction of so much native vegetation, there are many forests in Hawaii where one can expect to hear only the calls and songs of introduced birds. Moreover, there are some forests that, at times, appear to be completely devoid of birdlife. I have walked through such forests, hearing only the sounds of my own footsteps."

With this new, modestly priced edition "Hawaiian Birdlife" will continue to provide the people of Hawaii with an insight into their natural heritage. For readers elsewhere it remains the basic reference to the history and status of a unique avifauna.—Robert J. Raikow.

North American Game Birds and Mammals. By A. Starker Leopold, Ralph J. Gutiérrez, and Michael T. Bronson. Illus. by Gene M. Christman. Charles Scribner's Sons, New York, New York, 1981:198 pp., 137 illus., with captions, 113 range maps. $19.95.—The stated purpose of this book is to provide a companion reference to field guides that deal, at least in part, with game birds and mammals. The authors propose that it will be of value to hunters, wildlife biologists, students of natural resources, and others interested in learning about these species (e.g., bird-watchers and naturalists). A brief introduction deals with some basic concepts of habitat requirements and population dynamics of wildlife. The body of the text is apportioned into two major sections, birds and mammals. Within each section species are grouped taxonomically, and for each species (or group of closely related species), the range, habitat, and selected aspects of the life history are given. For birds, incubation periods, clutch-sizes, appearance of the species, and sex and age groups, and other comments, such as notes on behavior, specific habitat needs, diet, harvest figures, or hunting compose the "Remarks" section for each species; comparable information is provided for mammals. Illustrations include detailed pencil sketches of the animals, both male and female of sexually dimorphic species, and continental distribution maps. Many birds are shown in flight and there are a number of line drawings of physical characteristics and displays of birds. For mammals, a drawing of a skull typical of the family is included, as is the dental formula for each species. A glossary, bibliography, and index complete the book.

The text is well written in a comfortable, rather non-technical style with few grammatical errors. Distribution maps are very well done and are far more useful than those found in most field guides. Although only 105 citations are listed in the bibliography, the authors identified primary references for most species or groups. Generally, the life history infor-

mation about the 135 species is very accurate, although a few technical errors occur. For example, the lek mating system of Sage Grouse (*Centrocercus urophasianus*) may well be classical, but it is not as the authors describe. Unlike Prairie Chickens (*Tympanuchus* spp.) and Sharp-tailed Grouse (*T. phasianellus*), Sage Grouse tend to have multiple activity centers on a lek. It is curious that the authors included the Passenger Pigeon (*Ectopistes migratorius*) but ignored other recently extinct species or forms. The sketches, described by the publisher as "superb," in a number of instances fall well short of excellence, although patterns of plumage or pelage and proportions of animals are generally accurate. Some drawings, such as the display postures of grouse, are almost crude.

I believe that this book will be of interest to hunters and non-hunters alike. It could be useful in introductory level university courses dealing with game species, although its greatest utility is that of a reference rather than a text. It would not suffice as a text for advanced courses, and it would be of only limited value to the wildlife manager, scientist, or biologist.—John A. Crawford.

New Studies of Tropical American Birds. By Alexander F. Skutch. Illus. by Dana Gardner. Publ. Nuttall Ornithol. Club No. 19, Cambridge, Massachusetts, 1981:281 pp., 7 tables, 11 figs. $29.50.—To those already familiar with Skutch's "life histories," the present volume presents no novelties in terms of scope or approach: it consists of descriptions of the natural history and breeding biology of 27 species of (mostly) Costa Rican birds. For 22 species, the information consists of the updating or filling in gaps of previously published life histories, while Skutch publishes here for the first time on five species. For one of these (Rufous-winged Woodpecker [*Piculus simplex*]), his account is the first significant published description of its nesting behavior. For each of the updated accounts, a brief summary of previously published information is given and is most welcome as many of the older accounts are now out of print or difficult to obtain. The book is illustrated by Dana Gardner with pen-and-ink drawings of a number of the species discussed. Although not always entirely accurate with respect to details of shape and markings of the birds, these drawings definitely add to the attractiveness of the book. Skutch's writing is as graceful and articulate as ever, and the book is well printed on good paper, with very few typographical errors.

While one might cavil at this or that limitation (e.g., the lack of statistical analysis, the approach to aggressive behavior), this is to miss the main point of Skutch's contribution. This book should be judged not as an isolated work but as another step forward in its author's continuing studies of neotropical birds. These studies are providing a solid natural history data base that continues to serve as a stimulus and starting point for studies on ecology and behavior. As a worthy continuation of this unique and valuable enterprise, the present volume should be welcomed by all those with an interest in neotropical ornithology.—F. Gary Stiles.

Birds of the World: A Checklist. Third edition. By James F. Clements. Facts on File, Inc., New York, New York, 1981:xxxviii + 562 pp. $19.95.—Neither the first nor the second edition of this book was reviewed in The Wilson Bulletin. The reader is therefore referred to my review of the first edition in The Auk (92:821–824, 1975), as I shall be making comparisons between the first and third editions in the present review.

The body of Clements' book consists of a species list of birds of the world, with English and scientific names, a brief statement of distribution, and (new in this edition) a three-part numerical code (order, family, species), which the author suggests can be used for comput-

erization. Space is left under the distribution statement for each species for the owner to write in the date and location of a species' first sighting. Although the page size is 12 mm higher and 20 mm wider than in the first edition, a larger and coarser typeface has resulted in a less attractive page, with less space for notes.

Supplementary lists in this edition include "Major field guides and references" (author and title only); orders and families, with numerical codes and page references; "birds that have become extinct (or presumed extinct) since 1600"; [the following lists are presented under typographical subheads that make them appear to be part of the "extinct" category] "birds known from a single specimen (unique species)"; "birds known from such a small series that their status is in doubt"; "hypothetical and doubtful species"; "probable hybrids"; "probable races or subspecies"; species included that are omitted for various reasons from Morony, Bock, and Farrand's list; species listed by those authors but deleted by Clements.

Needless to say, these lists contain many errors and inconsistencies. To give only a few examples, Clements states in his text that *Muscicapa lendu* is known from one specimen from Zaire, but this species does not appear in his "known from one specimen" list, and the author overlooked the literature reference to the rediscovery of this species in Uganda in my review of the first edition. Incidentally, the index reference to *Muscicapa* directs the reader to pp. 375–376, whereas entries for this genus actually occupy pp. 387–388. I have no idea (nor any inclination to check) how many other indexing errors of this sort there may be.

There is no entry at all for the problematical *Phasmornis mystica* Oberholser, a hummingbird described from a unique holotype that cannot now be found (see Browning, Proc. Biol. Soc. Washington 91:89–90, 1978).

The list of "birds known from such a small series that their status is in doubt" is a hodgepodge. There is nothing "doubtful" about *Molothrus armenti* except whether to consider it conspecific with *M. aeneus*; Clements' statement that it is known from only two specimens from Leticia is incorrect (Friedmann, Auk 74:497–498, 1957). On the other hand, *Knipolegus subflammulatus* is no longer "doubtful" as it has been shown to be a plumage stage of *K. cabanisi* (Mayr, J. Orn. 112:313, 1971).

Clements has made several changes since the first edition, many no doubt in response to criticisms by reviewers. His partly alphabetical species sequence, for example, has been abandoned for (in general) the sequence provided by Morony, Bock, and Farrand. Yet his weird division of melanerpine woodpeckers between the genera *Melanerpes* and *Centurus*, taken from no known published list, taxonomically impossible, and mentioned specifically in my 1975 review, remains intact. Clements states in his introduction that he has now endeavored to separate breeding and winter ranges in the distribution statements, but the goose ranges I cited in my earlier review as "horrible examples" remain virtually unchanged, including the attribution of a Holarctic range to *Branta leucopsis*. The Eskimo Curlew (*Numenius borealis*) is one of the few shorebirds for which the summer and winter ranges are actually given separately, but the former is erroneously given as "Holarctic." More typical is the complete omission of the winter range, as in the Northern Phalarope, for which the entire distribution statement is "Circumboreal," or combined statements such as that for the Stilt Sandpiper (*Calidris himantopus*), "Arctic North America to South America." The Ruff (*Philomachus pugnax*) is inexplicably stated to be of "Wide distribution worldwide except for South America." My judgment is that the distribution statements have been very little improved over those in the first edition.

The general lack of quality control in this book is also manifested in the abundance of typographical errors (or misspellings). One "*Minus*" in the midst of *Mimus* spp. is an obvious typesetting error, but what are we to think of all three of the species of *Chlidonias* terns being listed as "*Cihlidonias*"? Typos turn up in the most embarrassing places: on p. xiv the

reader is directed to look up *Lacustroica* in the index and told that he will find *Lucustroica* there. Speaking of the index, Clements has tried to include "discontinued" genera as a service, stating that he has incorporated almost 600 in the index with a reference to their current generic names. Looking through Oberholser's "Bird Life of Texas," a current reference work notorious for use of obsolete genera, I found no fewer than 15 such names unindexed by Clements, and I only went as far as the end of the Anatidae.

Several rival "birds of the world" books have appeared since Clements' first edition, and each has strong and weak points. In spite of the change mentioned above, Clements' book still has perhaps the most attractive-looking pages, and his new numbering system may prove useful. However, the number of errors and inconsistencies detracts enormously from the value of the book. The acknowledgments section clearly implies that the only person who checked the entire manuscript was a graduate student. The concept of this book remains valid, so Clements and his publisher would be well advised to have the manuscript of any future edition scrutinized by a paid professional. Dr. Clements, although an experienced birder, is not a professional ornithologist, and there are many manifestations in his book of his limited knowledge, especially of the periodical literature. Even Dr. Clements, I am sure, must be appalled at the blatant naiveté of the publisher's blurb on the dust jacket that claims the author to be "one of a handful of naturalists to have seen and identified all known species of birds in their natural habitat"!—KENNETH C. PARKES.

WHERE TO FIND BIRDS IN NEW YORK STATE. By Susan Roney Drennan. Syracuse University Press, Syracuse, New York, 1981:499 pp., 106 maps. $38.00 cloth, $18.95 paper.—During one of my undergraduate summers I worked in the Rockies with a high school senior from Walla Walla, Washington, who truly believed that the entire state—not just city—of New York was paved over, a belief he attributed to one of his teachers. What a revelation for that teacher and that boy it would be to read Susan Drennan's new book! For their edification and that of any others with similar delusions, a recent U. S. Forest Service survey shows that New York State is now 61% forest, 22% farmland, and only 17% cities and suburbs. The presence in New York of those several major urban population centers, however, has provided the state with a large, dedicated, and knowledgeable corps of birders, organized into the Federation of New York State Bird Clubs, Inc. In the mid-1970's, the Federation's Executive Committee thought the time ripe for a comprehensive birding "Baedeker" for their state, and invited Susan Drennan, Associate Editor of American Birds, to write the text. In doing so, she has undoubtedly surpassed any similar book published for any other state or region of North America.

Among the eastern United States, New York is rivalled (possibly) only by North Carolina for diversity of bird habitats. New York's mountains are the southern outpost for such boreal species as the Three-toed Woodpecker (*Picoides tridactylus*) and Gray Jay (*Perisoreus canadensis*), and Long Island is the site of recent northward pioneering of breeding Chuck-will's-widows (*Caprimulgus carolinensis*) and Boat-tailed Grackles (*Quiscalus major*). The state borders on two of the Great Lakes and includes many smaller lakes and several major rivers. On Long Island and satellite islands are some of the most important northeastern colonies of herons, ibises, terns, and other water birds.

The book begins with brief introductory chapters (New York State Avian Records Committee, New York State Rare Bird Alerts, Ornithological Collections and Libraries, Physiographic Regions), followed by a section for each of the ten regions of the state recognized in the Federation's journal, The Kingbird, and additional chapters on "Seabirds and Pelagic Birding," and "Hawk Migration." Needless to say, Mrs. Drennan relied heavily on information and advice from regional experts, and these are duly acknowledged.

Obviously, this is not a book to read, but to use. I read one chapter thoroughly as a sample—that on the Finger Lakes (Region 3), an area that I once thought I knew well. I was amazed at the detailed information given about birding areas that I had often visited and others of which I had never heard. It is obvious that knowledge of the local distribution of birds has expanded tremendously since I covered Region 3 for The Kingbird in 1951 and 1952. Each region is introduced with a general description, mentioning its outstanding geological and vegetational features, and the birding information for each of the localities is often interspersed with comments on ferns, flowers, and trees. Each locality is rated on a * to **** scale for birding possibilities in each of the four seasons, and detailed directions are given for finding the best spots for particular groups of birds. Localities are indexed, and there is a taxonomically arranged index to bird species, giving their breeding or occurrence status for each of the regions.

Each chapter is illustrated with maps, the first a general map of the region showing not much more than county boundaries and the approximate location of principal birding areas, shown in more detail on additional maps of various scales. My only serious criticism of the book refers to distances; none of the maps has a scale of miles or kilometers. Although driving distances are often given in the text, they are equally often omitted; natural features, road intersections, and other landmarks are mentioned without indicating how far one must drive before beginning to watch for the landmark. I know from experience that this can often result in overshooting the mark, especially in heavy traffic on major roads.

Although the price of the hard-bound edition is a bit steep, I recommend its purchase by birders residing in or frequently visiting New York. Judging from the review copy, I doubt that the relatively lightweight covers of the paperback edition will stand up under the kind of use that this book will certainly and deservedly get.—Kenneth C. Parkes

The Effect of Weather on Avian Mortality. By James A. Gessaman and Gary L. Worthen. Privately published, 1982:173 pp., paper covers. $12.00.—This book is a source of information from the literature on the relationships between weather and avian mortality. The bulk of the text consists of abstracts of 223 papers on the subject. Access to this literature compilation is provided by indexes of key words in their titles, authors and co-authors, year of publication, geographical location, and species. The authors do not claim to have exhausted the literature in their survey, and request that readers provide additional references for a planned supplementary volume. To obtain a copy send a check payable to James A. Gessaman, UMC 53, Utah State University, Logan, Utah 84322.—R.J.R.

A Bibliography of Alberta Ornithology. By Martin K. McNicholl, Philip H. R. Stepney, Peter C. Boxall, and David A. E. Spalding. Provincial Museum of Alberta, Natural History Occasional Paper No. 3, 1981:377 pp., paper cover, price not given.—This compilation includes a history of ornithology in Alberta, a check-list of Albertan birds with habitat, abundance, and status information, a list of sources, and indices to authors and bird species. The bulk of the work consists of the bibliography itself, with listings grouped under ten subject headings: Nomenclature and Taxonomy; Distribution and Migration; Paleontology, Archeology and Extinct Birds; Morphology and Physiology; Ecology and Life History; Disease and Parasitology; Management and Conservation; Bibliographic Profiles; Miscellaneous; and Semi-popular. Copies may be obtained by writing to: Provincial Museum of Alberta, Alberta Culture, 12845–102 Avenue, Edmonton, Alberta T5N 0M6, Canada.—R.J.R.

PROCEEDINGS OF THE SIXTY-THIRD ANNUAL MEETING

CURTIS S. ADKISSON, SECRETARY

The Sixty-third Annual Meeting of The Wilson Ornithological Society was held Thursday, May 6 to Sunday, May 9, 1982, at Virginia Polytechnic Institute and State University, Blacksburg, Virginia. The hosts for the meeting were the University and the New River Valley Bird Club. Curtis S. Adkisson chaired the local arrangements committee. One hundred fifty-six people attended the meeting.

The meeting opened with registration Thursday evening followed by a wine and cheese reception in the Donaldson Brown Center for Continuing Education on the campus of the University. On Friday morning, following a pre-breakfast field trip, the Society was welcomed by Dr. John D. Wilson, University Provost. President Abbot S. Gaunt responded for the Society. After the first business meeting, the paper sessions began.

The annual banquet was held in the Donaldson Brown Center on Saturday night. Immediately following the banquet, Mr. Adger Smyth on Charlotte, North Carolina, gave a presentation in memory of the late Frederick Kent Truslow featuring Mr. Truslow's photography. Included were some of his most famous bird photographs.

At the banquet, President Gaunt announced the following awards:

EDWARDS PRIZES (for best papers appearing in *The Wilson Bulletin* in 1981)

(1) First Edwards Prize to C. John Ralph, "Age ratios and their possible use in determining autumn routes of passerine migrants," Wilson Bull. 93:164–188.
(2) Second Edwards Prize to Peter G. Merritt, "Narrowly disjunct allopatry between Black-capped and Carolina chickadees," Wilson Bull. 93:54–66.

MARGARET MORSE NICE AWARDS

Michael E. Facemire, Mesa, Arizona, "An investigation of the relationships between winter precipitation and nesting success in the Black-throated Sparrow."
A. Townsend Peterson, Oxford, Ohio, "The breeding biology of the Upland Sandpiper in Ohio."

LOUIS AGASSIZ FUERTES AWARDS

Stephen Nowicki, Cornell University, "Physiology and physics of harmonically complex bird calls: a comparative study."
Brian J. McCaffery, Cornell University, "Parental care in the Mountain Plover (*Charadrius montanus*)."

STEWART AWARDS

Tod DeLong, Brigham Young University, "Nocturnal behavior in nesting Long-eared Owls (*Asio otus*)."
Charles F. Facemire, Arizona State University, "Social regulation in an emberizine finch, *Piplo aberti:* an investigation of cause and effect."
Patricia Ann Greenleaf, University of Arkansas, "Blackbird and starling behavior in a northwest Arkansas roost."

Kathleen D. Groschupf, Virginia Polytechnic Institute and State University, "Song repertoires and singing behavior of Rufous-winged and Cassin's sparrows: preliminary research on the functional significance of diverse singing strategies in *Aimophila* sparrows."

David G. Krementz, University of Western Ontario, "Energetics of breeding House Sparrows (*Passer domesticus*)."

Patricia McGill-Harelstad, Cornell University, "Cold exposure and cold tolerance of Great Black-backed and Herring gull chicks—a possible factor in the displacement of a species."

James F. Quinn, University of Oklahoma, "Evolution of sexual dimorphism in body size of a monogamous bird: a comparative study of Black Skimmers and Caspian Terns."

Douglas Runde, Wyoming Cooperative Wildlife Unit, "Nest-site fidelity of Prairie Falcons in relation to strip mining activity in southwestern Wyoming."

Roland R. Roth, University of Delaware, "Between year dispersal by adult and juvenile Wood Thrush."

Jill M. Trainer, University of Michigan, "Song dialects, communication, and social organization in Chestnut-headed Oropendolas (*Varhynchus wagleri*) and Yellow-rumped Caciques (*Cacicus cela*)."

ALEXANDER WILSON PRIZE (for best student paper at the meeting)

Elizabeth Litovich, Rutgers University, "Communication and allocation of parental care in Starlings."

There were field trips to Poverty Hollow in the Jefferson National Forest, to Mabry Mill on the Blue Ridge Parkway, and local trips to the Smithfield Plantation, and the Duck Pond area on campus. On Sunday there was a half-day trip to Mountain Lake on the summit of Salt Pond Mountain. Participants went birding around the shore of Mountain Lake, had breakfast at the Mountain Lake Hotel, then visited the Mountain Lake Biological Station and a U.S. Forest Service scenic area with a virgin stand of eastern hemlocks.

FIRST BUSINESS MEETING

The first business meeting was held on 7 May 1982, and was presided over by President Abbot S. Gaunt. He announced the posting of a list of new members, and the appointment of the Alexander Wilson Prize Committee. He also announced that William A. Klamm, Robert A. Whiting, and Hubert P. Zernichow would serve as the Auditing Committee. He noted also that persons interested in submitting resolutions for consideration should give these to Kathleen Anderson or Joanna Burger. Secretary Curtis S. Adkisson then summarized actions taken by the Council at its 1982 meeting on 6 May. These included the announcement that Jon C. Barlow was re-elected Editor of *The Wilson Bulletin*, Treasurer Robert D. Burns gave the Treasurer's Report.

REPORT OF THE TREASURER
1 JANUARY 1981 TO 31 DECEMBER 1981

GENERAL FUNDS

RECEIPTS

Dues collected in 1981		
Student and Regular Membership for 1981	$ 11,078.05	
For 1982	14,372.50	
Family Membership for 1981	110.00	
For 1982	396.00	
Sustaining Membership for 1981	1,733.00	
For 1982	1,634.00	
TOTAL DUES		$ 29,323.55
Subscriptions to *The Wilson Bulletin*		
For 1981	$ 5,706.50	
For 1982	7,358.76	
TOTAL SUBSCRIPTIONS		$ 13,065.26
Back issues of *The Wilson Bulletin*		$ 770.50
Interest and Dividends		$ 17,456.13
Royalties		$ 832.27
Contributions from Authors		$ 5,018.19
Balance of General Funds Transferred from Old Kent Bank		$ 7,904.86
Contributions to the Student Awards Funds		$ 6,271.19
Contributions to Endowment and Life Memberships		$ 10,647.00
Balance of Endowment Funds Transferred from Old Kent Bank		$ 5,633.50
TOTAL RECEIPTS—Jan. 1–Dec. 31, 1981		$ 96,922.45

DISBURSEMENTS

The Wilson Bulletin		
December 1980	$ 9,451.27	
March 1981	9,064.11	
June 1981	10,631.35	
September 1981	10,347.57	
Colorplates	2,765.21	
Insurance	23.00	
Back orders $ names lists	176.83	
Editorial Assistants	1,000.00	
TOTAL COSTS		$ 43,459.34
Additions to Endowment Trust at Central Counties Bank		$ 13,511.50
Deposit of Student Awards Funds to Dreyfus Liquid Assets		$ 6,271.19
Deposit to Awards Funds from Endowment Earnings		$ 2,200.00
1981 Incorporation Fee		$ 5.00
Dues to International Council for Bird Preservation 1981		$ 100.00
Editor's Expenses		
Telephone		$ 160.86
Attend Allen Press Conference		$ 316.64
Treasurer's Expenses		
Postage and Secretarial Service		$ 245.00
Miscellaneous Printing Costs		$ 69.67

Membership Committee—New Brochures	$ 127.58
Ornithological Societies of North America	$ 9,157.23
Treasurer's Bond	$ 37.00
Audit and Legal Fees for 1977–1979	$ 2,101.03
TOTAL DISBURSEMENTS—Jan. 1–Dec. 31, 1981	$ 77,762.04
1981 INCOME SURPLUS	$ 19,160.41

CASH ACCOUNTS

Checking Account, 31 December 1981	$ 3,525.71	
Savings Account, 31 December 1981	49.24	
Dreyfus Liquid Assets, 31 December 1981	38,778.83	
TOTAL CASH ON HAND		$ 42,353.78

DESIGNATED ACCOUNTS

Van Tyne Memorial Library Fund

RECEIPTS		
Balance 1980	$ 1,174.58	
Sales and Gifts	273.02	
DISBURSEMENTS		
Purchase of Books	$ 883.05	
BALANCE		$ 564.45

Louis Agassiz Fuertes Research Fund

RECEIPTS	
Endowment Earnings	$ 200.00
DISBURSEMENTS	
Mark K. Wourms	$ 200.00

Margaret Morse Nice Fund

RECEIPTS	
Endowment Earnings	$ 100.00
DISBURSEMENTS	
Linda Heald	$ 100.00

Alexander Wilson Prize

RECEIPTS	
Endowment Earnings	$ 100.00
DISBURSEMENTS	
H. Carolyn Peach	$ 100.00

Ernest P. Edwards Prize

RECEIPTS	
E. P. Edwards	$ 350.00
DISBURSEMENTS	
M. Ross Lein (donated to student awards)	$ 225.00
James F. Wittenberger	$ 125.00

Paul A. Stewart Awards

RECEIPTS		
Endowment Earnings	$ 1,400.00	
DISBURSEMENTS		
Kenneth F. Abraham	$ 200.00	
David E. Blockstein	200.00	
Roger L. Boyd	200.00	
Shari Hahn	200.00	
Katherine J. Kuletz	200.00	
Thomas E. Martin	200.00	
Joseph M. Wunderle	200.00	

Aaron Bagg Student Award Fund

RECEIPTS		
Balance from 1980	$ 30.00	
Gift	200.00	
DISBURSEMENTS		
16 Student Memberships Awarded	$ 224.00	
BALANCE		$ 6.00

Annual Meeting Reserve Fund

RECEIPTS		
Balance from Corpus Christi Meeting	$ 225.13	
Balance from Sackville Meeting	116.87	
DISBURSEMENTS		
Local Committee—Sackville	$ 150.00	
BALANCE		$ 222.00

Endowment

RECEIPTS		
Value of General Endowment Fund 31 Dec. 1980	$164,973.29	
Life Membership Payments and Gifts	13,511.50	
Depreciation of Principal	(1,893.63)	
Value of General Endowment Fund 31 Dec. 1981		$149,469.91

George M. Sutton Colorplate Fund

PRINCIPAL	$ 27,121.25

Total Combined Wilson Ornithological Society Endowment Funds 21 Dec. 1981	$176,591.16
Earnings from Endowment for 1981	$ 17,456.13

SECOND BUSINESS MEETING

The second business meeting was called to order by President Gaunt on Saturday afternoon, 8 May 1982. The proposed new members of the Society were elected unanimously. Three resolutions presented by the Resolutions Committee were approved unanimously, as was the report of the Auditing Committee. These and other summaries of committee reports to Council are presented below.

AUDITING COMMITTEE REPORT—1981

We, the undersigned, have examined the Treasurer's records, bank statements, cancelled checks, and other financial records of the Society covering the period from 1 January 1981 to 31 December 1981. Our examination confirms that receipts and disbursements have been correctly accounted for, and bank balances are in agreement with the Treasurer's statement.

Hubert P. Zernichow, *Member*
Robert A. Whiting, *Member*
William A. Klamm, *Member*

EDITOR'S REPORT—1981

The staff of *The Wilson Bulletin* processed 211 manuscripts in 1981, including the 145 received during the year. Volume 93 contained 32 major papers, 56 short papers, 61 pages of book reviews and notices, a lengthy conservation report, an annual report, and other short notices, for a total of 624 pages. There are plans for color plates for all issues in 1982, but plans for future color plates are less certain.

Some suggested improvements for the future include: review articles on a variety of subjects such as art, field techniques, museum practices, anatomical surveys; informing potential authors that we no longer have mandatory page charges; adding to the list of referees who will review papers without advance notification; faster revision of papers by authors.

I have been greatly assisted by many people in the editorial office and elsewhere. These include: Assistant Editor Margaret May; Senior Editorial Assistants Gary Bortolotti and Nancy Flood; Editorial Assistants Dave Ankney, Keith Bildstein, Jim Rising, and Richard Snell; the staff of Allen Press, especially Arly Allen, Ken Blair, John Breithaupt, and Guy Dresser; the Royal Ontario Museum and its staff, especially R. D. James, M. May, and Janet Mannone; members of the Society who helped out in many ways, especially Clait Braun, Sandra Gaunt, Toby Gaunt, Jerry Jackson, Bill Lunk (color plates), Bob Raikow (book reviews), and Peter Stettenheim. I thank also the 150 colleagues who reviewed manuscripts for us during the year.

Jon C. Barlow, *Editor*

LIBRARY COMMITTEE REPORT—1981

The Josselyn Van Tyne Memorial Library operated as usual in 1981, with increases in certain activities and decreases in others. Notably, our file of translations is expanding, and being computerized. Through exchanges, we received 150 journals, newsletters, and reprints. Together with 35 gifts and complimentary subscriptions, and five regular subscriptions, there are 190 periodical titles. Fifty-eight members borrowed 742 items during the year. We hope that publication of a book list in 1982 will lead to greater use. During 1981 we received 809 items, including 27 books and reports, 510 reprints, 236 journal issues, and 36 translations. We thank the following for their donations: A. J. Berger (514 of the above), J. Cheek, J. J. Dinsmore, S. M. Goodman, J. Haffer, P. Hamel, J. Hinshaw, H. Hoogstraal, C. S. Houston, L. Kelso, C. M. Kirkpatrick, F. Lohrer, H. Mayfield, B. G. Murray, Jr., J. C. Nicholson, F. Novaes, M. S. Putnam (for International Crane Foundation), W. J. Richardson, R. Roth, D. Siegel-Causey, A. Simon, G. A. Smith, M. Snow, J. G. Strauch, Jr., and Col. L. R. Wolfe.

The committee once more thanks the entire membership. The Library belongs to us all; let's continue to support and use it.

William A. Lunk, *Chairman*

MEMBERSHIP COMMITTEE COMMITTEE REPORT—1981

Total paid membership for the Society was 2257 in the calendar year of 1981. The figure for 1982 is not yet available. My office handled a total of 14 requests for membership applications since the last meeting. Applicants were sent (1) our prospectus and dues structure and (2) a letter asking that dues be sent to OSNA in Columbus, Ohio. I encourage anyone interested in distributing our new prospectus to potential new members to write me.

Keith L. Bildstein, *Chairman*

STUDENT MEMBERSHIP COMMITTEE REPORT—1981

Announcement of the availability of the Aaron M. Bagg Student Membership Awards was made in *The Wilson Bulletin* and the Ornithological Newsletter. In the absence of funds designated for the solicitation of nominees from among the membership, for the first time no letters were sent to selected members seeking the names of students. In response to letters of inquiry, 31 sets of application materials were sent out. There were 13 eligible applicants for the Bagg Award, about a third as many as in the past year. The members of the committee evaluated the nominees independently, and there was complete agreement on the high quality of all applicants. The following received Aaron M. Bagg Student Membership Awards: Anthony H. Bledsoe, Yale Univ.; Petra G. Bohall, Univ. Florida; Bruce A. Colvin, Bowling Green State Univ.; William E. Davis, Univ. California-Davis; James G. Devereux, Frostburg State College; Sharon Goldwasser, Univ. Arizona; Michael E. Kaspari, Univ. Nebraska; Francis P. Kehoe, Univ. Western Ontario; Mary C. McKitrick, Univ. Pittsburgh; Mari B. Smaby, North Dakota State Univ.; Ellen J. Snyder, Univ. Maine-Orono; Robert E. Szafoni, Univ. Illinois; Brian M. Winter, Iowa State Univ.

John L. Zimmerman, *Chairman*

REPORT OF THE RESOLUTIONS COMMITTEE

The following resolutions were read during the second business meeting:

WHEREAS, the continued existence of mankind as well as all forms of life depends upon healthy ecosystems in which all the components from the smallest microbes to the largest plants and animals play crucial and interdependent roles, and

WHEREAS, we are only beginning to understand the complexities of these relationships and our dependence upon this diversity of life forms, and

WHEREAS, the Endangered Species Act is widely considered to be one of the most important wildlife conservation laws in the world,

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society urges the Congress of the United States to reauthorize a strong Endangered Species Act as a means of insuring that this generation does not callously or carelessly destroy essential links in the web of life before we fully understand their parts in sustaining all life on this planet.

WHEREAS, scientists have shown beyond doubt that our coastal bays, estuaries, marshes, and barrier islands are of inestimable value in maintaining viable populations of shellfish, finfish, birds, and other wildlife, and

WHEREAS, the laws, regulations, and accepted uses impacting these coastal areas are a tangled web of contradictory forces simultaneously attempting to alter, develop, and protect these fragile ecosystems, and

WHEREAS, the U. S. Fish and Wildlife Service has identified in 'concept plans' nearly 50 barrier islands along the Atlantic and Gulf coasts that have exceptional value for fish and wildlife, and

WHEREAS, we believe that federal subsidies should be cut off for developing these unstable, storm-prone areas, thereby minimizing the risks and threats to human life and property, while simultaneously perpetuating wild, living resources, including bird populations and their habitats, and

WHEREAS, the Reagan administration hopes to 'zero fund' the Coastal Zone Act which was renewed in 1980,

THEREFORE BE IT RESOLVED, that The Wilson Ornithological Society urgently requests the House and Senate Appropriations Committees to fully recognize the special ecological and biological characteristics of our barrier islands and coastal zones and to further recognize that any weakening of the Coastal Zone Act will not only have a deleterious effect upon fisheries and wildlife of economic and aesthetic importance but will also, when the inevitable storms destroy homes and businesses built in these hazardous areas, prove far more costly than enforcing the present Coastal Zone Act.

WHEREAS, The Wilson Ornithological Society has held its 63rd annual meeting in Blacksburg, Virginia, 6 through 9 May 1982, at the invitation of Virginia Polytechnic Institute and State University and the New River Valley Bird Club, and

WHEREAS, the quality of the scientific programs, the warm hospitality, and superb organization provided by Curtis Adkisson and the Local Committee, and the comfortable accommodations at the Donaldson Brown Center for Continuing Education at Virginia Polytechnic Institute and State University combined to make this an excellent meeting,

THEREFORE BE IT RESOLVED that The Wilson Ornithological Society expresses its gratitude and thanks to Curtis Adkisson and his Local Committee on Arrangements, to Clait Braun and Ronald Ryder, who organized the Scientific Program, and to the staff of the Donaldson Brown Center for the planning and hard work which has made this such an enjoyable and worthwhile meeting.

NOMINATING COMMITTEE REPORT—1981

The second business meeting ended with the report of the Nominating Committee, chaired by George A. Hall. He presented the slate of officers for the 1982–83 year: President, Abbot S. Gaunt; First Vice-President, Jerome A. Jackson; Second Vice-President, Clait E. Braun; Secretary, Curtis S. Adkisson; Treasurer, Robert D. Burns; Elective Member of the Council (term to expire in 1985), Anthony J. Erskine. There being no further nominations, it was moved, seconded and passed that the Secretary be instructed to cast a unanimous ballot for the slate.

PAPERS SESSION

The papers session was organized by Clait E. Braun and Ronald A. Ryder. The individual sections were chaired by: C. S. Adkisson, J. C. Barlow, K. Bildstein, C. E. Braun, M. H. Clench, M. W. Collopy, R. N. Conner, T. C. Grubb, J. A. Jackson, D. W. Johnston, B. Schardien, J. Sheppard, R. B. Stiehl, and G. E. Woolfenden. A list of papers presented follows.

Stuart D. Strahl, State University of New York at Albany, "Observations on the social system and foraging ecology of the Hoatzin in the llanos of Venezuela."

C. P. L. Barkan, J. L. Craig, S. D. Strahl, A. M. Stewart, and J. L. Brown, State University of New York at Albany, "Dominance in social units of communal Mexican Jays."

G. E. Woolfenden and J. W. Fitzpatrick, University of South Florida and Field Museum of Natural History, "Testing the territorial budding hypothesis."

Michael W. Collopy, University of Florida, "Food habits of Golden Eagles: a comparison of two techniques."

Kenneth D. Meyer, University of North Carolina, "Sexual size dimorphism and niche separation in breeding Sharp-shinned Hawks (*Accipiter striatus*)."

Lenora Oosterhuis and Anthonie M. A. Holthuijzen, V.P.I. & S.U., and Mark R. Fuller, U.S. Fish and Wildlife Service, "Migration behavior and habitat use of immature female Sharp-shinned Hawks (*Accipiter striatus*)."

Keith L. Bildstein, Winthrop College and Baruch Institute for Marine Biology, University of South Carolina, "Sex dependent differences in the hunting behavior and parental care of Northern Harriers breeding in Wisconsin."

Petra G. Bohall, University of Florida, "Winter habitat use by American Kestrels in Florida."

Judith W. McIntyre, Utica College of Syracuse University, "Nurseries: habitat requirements during the early chick-rearing period."

James F. Parnell, University of North Carolina at Wilmington, "Populations and breeding biology of the Eastern Brown Pelican (*Pelecanus occidentalis carolinensis*) in North Carolina."

Gary R. Hepp, North Carolina State University, "In support of behavioral dominance as a mechanism influencing segregation of the sexes in wintering waterfowl."

R. T. DiGiulio and P. F. Scanlon, V.P.I. & S.U., "Heavy metals in Chesapeake Bay waterfowl."

Nancy S. Mueller, North Carolina Central University, "Induction of immunological tolerance in Mallards."

Helmut C. Mueller, University of North Carolina, Chapel Hill, "Functions of reversed sexual dimorphism in *Sula*."

Wayne Hoffman, University of South Florida, "Seasonal distribution of terns off the coasts of Florida."

Thaddeus A. Grudzien, Central Michigan University, "Breeding sounds of the Common Snipe: description and proposed functions."

Peter W. Hicklin, Canadian Wildlife Service, "Migrant Semipalmated Sandpipers in the Bay of Fundy: predator-prey interactions, fat deposition, and turnover rate."

Jerome A. Jackson and Bette J. Schardien, Mississippi State University, "Distribution, status, and nesting phenology of Snowy Plovers in Mississippi."

Julie A. Hovis, University of Florida, "Population biology and habitat characteristics of Red-cockaded Woodpeckers in northern Florida pine forests."

Steven Martindale, State University of New York at Albany, "Sexual dimorphism in size, foraging, and aggression in Gila Woodpeckers."

Annie P. Marshall, University of the Pacific, "Courtship and reproduction in the Bali Mynah (*Leucopsar rothschildi*) (Aves: Sturnidae)."

Harlo H. Hadow, Coe College, "Song patterning and discrimination in Northern and Southern house wrens."

Mary E. Anderson and Richard N. Conner, Stephen F. Austin State University and U.S. Forest Service, "Dialects and syllable structure of three east Texas Cardinal populations."

Gary Ritchison, Eastern Kentucky University, "The function of singing by female Black-headed Grosbeaks."

John W. Hardy, Ben B. Coffey, Jr., and Lula Coffey, Florida State Museum, "A mystery nightjar in Peru—what is it anyway?"

Callyn D. Yorke, University of Arkansas, "A comparison of avian community structure in a rubber-tree plantation and an adjacent suburb of Kuala Lumpur, Malaysia."

David W. Johnston, George Mason University, "Ecological analysis of a long-term breeding bird community."

Charlie W. Wooten, University of Arkansas, "Avian distribution, abundance, and habitat associations in northwestern Arkansas."

Daniel R. Petit, Ohio State University, and Kenneth E. Petit, Kent State University, "On foliage height diversity and atmospheric moisture as factors controlling diversity and distribution of birds in temperate deciduous forest."

Joseph M. Meyers, University of Georgia, "On environmental factors and avian communities in the Okefinokee Swamp, Georgia."

Charles R. Preston, University of Arkansas, "Breeding territory size and space utilization in the Tufted Titmouse."

Jon C. Barlow and Brete G. Griffin, Royal Ontario Museum and University of Toronto, "Comparative habitat use and foraging in breeding and wintering Gray Vireos in west Texas."

Philip C. Shelton, Clinch Valley College, "Northern birds on Mt. Rogers, Virginia."

Theresa Duffey, University of Wisconsin—Green Bay, "Gray Partridge: upland game bird of the future?"

George H. Haas, U.S. Fish and Wildlife Service, "Nesting effort of individual Mourning Dove pairs in Georgia."

Joseph M. Wunderle, Jr., North Carolina State University, "The timing of the breeding season in the Bananaquit (*Coereba flaveola*) on Grenada, West Indies."

Elizabeth Litovich, Rutgers University, "Communication and allocation of parental care in Starlings."

G. T. Bancroft, University of South Florida, "Evolution of asynchronous hatching in the Boat-tailed Grackle."

Kent L. Fiala, SUNY, Stony Brook, "Female-biased nestling ratio in a Red-winged Blackbird population."

E. K. Bollinger and J. W. Caslick, Cornell University, "Relationships between Red-winged Blackbird feeding activity and northern corn rootworm beetles in field corn in central New York."

A. M. A. Holthuijzen and Curtis S. Adkisson, V.P.I. & S.U., "Feeding, digestion, and seed germination enhancement of eastern red cedar (*Juniperus virginiana* L.) by Cedar Waxwings (*Bombycilla cedrorum* L.)."

Charles Walcott, Cornell University, "Homing pigeon navigation: do they use the Earth's magnetic field?"

Christine M. Lucia and David R. Osborne, Miami University, "Sunset as an orientation cue in White-throated Sparrows."

Harry E. LeGrand, Jr., Clemson University, "An hypothesis of redetermined migration: flying on calm nights to correct for displacement."

Kimberly G. Smith, University of Arkansas, "Avian foraging behavior along a montane sere in northern Utah."

Thomas C. Grubb, Jr., Ohio State University, "Sparrows and a brushpile: foraging responses to different combinations of risk and energy cost."

Andrew D. Thompson, Jr. Ohio State University, "Laboratory foraging responses of woodland birds to the presence of conspecifics and heterospecifics."

Mercedes C. Mondecar, University of Arkansas, "Effect of a conspecific on the activity pattern of the White-throated Sparrow (*Zonotrichia albicollis*)."

A. Cyr, G. Michaud, and G. Groulx, Sherbrooke University, "The advantages of fooling the system through mimicry: Redstart case study."

Richard R. Repasky, North Carolina State University, "An assessment of a home range sampling scheme."

A. B. Carey, USDA Forest Service, "Line-transect sampling of cavity-using birds."

Robert L. Paterson, Jr., and Margaret S. Paterson, Frostburg State College, "An application of the James-Shugart habitat sampling method to measure nest-sites."

Richard N. Conner, James G. Dickson, and J. Howard Williamson, USDA Forest Service, "Comparisons of two census techniques and mist net captures."

Antoinette L. Pepin, Utah State University, "Molt schedules of Mountain and Black-capped chickadees."

J. D. Rising, University of Toronto, "The progress of oriole hybridization in Kansas."

Thomas G. Balgooyen, San Jose State University, "Environmental correlates of avian coloration in breeding males."

T. David Pitts, University of Tennessee at Martin, Eastern Bluebird nest-site fidelity and mate fidelity in northwest Tennessee."

POSTER PAPERS

Paul B. Hamel, Jeffrey L. Beacham, and Anna E. Ross, Clemson University, "A laboratory study of cranial pneumatization in Indigo Buntings."

Tom Webber, Florida State Museum, "Allopreening by Brown-headed Cowbirds."

R. Todd Engstrom, Robert L. Crawford, and W. Wilson Baker, Florida State University and Tall Timbers Research Station, "Bird populations in relation to forest structure following fire exclusion: a 15-year study."

ATTENDANCE

ARKANSAS: *Fayetteville*, Robin R. Buff, Patricia Ann Greenleaf, Mercedes Mondecar, Charles R. Preston, Kimberly Smith, Charles Wooten, Callyn D. Yorke.

CALIFORNIA: *San Jose*, Thomas G. Balgooyen.

COLORADO: *Aurora*, Thomas Muir; *Fort Collins*, Clait E. Braun; *Golden*, James Tate, Jr.

DISTRICT OF COLUMBIA: Richard C. Banks, Carol Lutyk, Linda Lyon, Jay Sheppard, Jeff Swinebroad.

FLORIDA: *Gainesville*, Petra Bohall, Mary H. Clench, Michael Collopy, John William Hardy, Julie Hovis, Robert Repenning, Tom Webber; *Lake Placid*, Fred Lohrer; *Tampa*, G. Thomas Bancroft, Wayne Hoffman, Glen Woolfenden, Jan Woolfenden; *Tallahassee*, Robert L. Crawford, Todd Engstrom.

GEORGIA: *Athens*, Joseph M. Meyers; *Watkinsville*, George H. Haas.

INDIANA: *Hannover*, J. Dan Webster.

IOWA: *Cedar Rapids*, Harlo H. Hadow.

KENTUCKY: *Richmond*, Gary Ritchison.

MAINE: *Wayne*, Mrs. Andrew Dawson, Olin S. Pettingill, Jr.

MARYLAND: *Bethesda*, Shirley Briggs, Eileen Williams; *Frostburg*, Robert L. Paterson, Jr.; *Gaithersburg*, Jean Swinebroad.

MASSACHUSETTS: *Manomet*, Kathleen Anderson; *Worcester*, Susan Berman.

MICHIGAN: *Grass Lake*, Harold Ratcliff; *Jackson*, Robert Whiting; *Pleasant Lake*, Hugh Zernichow.

MISSISSIPPI: *Mississippi State*, Jerome A. Jackson, Bette Schardien.

NEW JERSEY: *New Brunswick*, Elizabeth Litovich, Michael Lombardo, Harry Power.

NEW YORK: *Albany*, Chris Barkan, Steve Martindale, Stuart D. Strahl; *Ellenville*, Barbara Belanger, Valerie Freer; *Ithaca*, Eric Bollinger, Charles R. Smith, Charles Walcott; *Slingerlands*, Walton B. Sabin; *Utica*, Judith McIntyre.

NORTH CAROLINA: *Chapel Hill*, Kenneth O. Horner, Ken Meyer, Nancy Mueller, Helmut Mueller; *Four Oaks*, Thomas Haggerty; *Mars Hill*, Alan B. Smith; *Raleigh*, Phillip D. Doerr, Gary Hepp, Dick Repasky, Joseph Wunderle; *Wilmington*, Frances Parnell, James F. Parnell.

OHIO: *Athens*, John C. Ritzenthaler, Sally C. Ritzenthaler; *Columbus*, Gail Foreman, Abbot

Gaunt, Sandra Gaunt, Thomas C. Grubb, Jr., Ann Marshall, Dan Petit, Andrew Thompson; *Canfield*, G. William Richter; *Gambier*, Robert D. Burns; *Hudson*, Neil Henderson; *Lakewood*, Nancy R. Klamm, William A. Klamm; *Oxford*, Christine Lucia.

PENNSYLVANIA: *Chester Springs*, Babs Street, Phillips Street; *Edinboro*, Donald B. Snyder; *Johnstown*, Joseph Patterson, Lora Patterson; *Pittsburgh*, Nancy Lopez, Jay Loughlin, Mary McKitrick, Ellen Parkes, Kenneth Parkes.

SOUTH CAROLINA: *Chester*, Mary Lee Robinson, Mrs. W. C. Stone, Sr.; *Clemson*, Jeffrey L. Beacham, Carl Helms, Harry LeGrand, Anna Ross; *Rock Hill*, Keith Bildstein; *Spartanburg*, Miller Foster.

TENNESSEE: Dale K. Fowler; *Martin*, David Pitt; *Maryville*, Ralph Zanglein; *Norris*, Charles Nicholson, Linda J. Turner.

TEXAS: *Nacadoches*, Richard N. Conner.

VIRGINIA: *Arlington*, James Felkel; *Blacksburg*, Curtis Adkisson, Anita Allen, Mary Anderson, Cathy Blohowiak, Kenneth Cooper, Gerald Cross, Nina Fraser, Thaddeus Grudzien, A. M. A. Holthuijzen, Rosemary Norris, L. Oosterhuis, Mary Linda Smyth, Linda Stover, Jerry Via; *Chincoteague*, Irvin Ailes, Stan Shutek; *Fairfax*, David W. Johnston, Esta Johnson; *Glen Allen*, Kathryn Schneider; *Harrisonburg*, A. Clair Mellinger; *Manassas*, Roxie Laybourne; *Parksley*, Karen Terwilliger; *Scottsville*, Mrs. Frederick S. Whiteside; *Sterling*, Antoinette Pepin; *Virginia Beach*, Kimberly Young; *Williamsburg*, Ruth Beck, Sherwin Beck, Mitchell Byrd.

WEST VIRGINIA: *Morgantown*, Dr. and Mrs. Maurice Brooks, Andrew Carey, George A. Hall; *St. Albans*, Brian D. Watts.

WISCONSIN: *Green Bay*, Teresa Duffey, Richard Stiehl; *Wisconsin Rapids*, Jeff Groth.

NEW BRUNSWICK: *Sackville*, Peter Hicklin.

ONTARIO: *Toronto*, Jon C. Barlow, James D. Rising.

QUEBEC: *Sherbrooke*, Andre Cyr.

UNITED KINGDOM: *Tring*, Alan Knox.

1983 ANNUAL MEETING

The 1983 Annual Meeting of The Wilson Ornithological Society will be held in Green Bay, Wisconsin 2–5 June 1983. The host for the meeting is the University of Wisconsin–Green Bay. Dr. Richard B. Stiehl is Chairman of the Local Arrangements Committee. His address is *College of Environmental Sciences, University of Wisconsin–Green Bay, Green Bay, Wisconsin 54302.*

INDEX TO VOLUME 94, 1982

By Janet T. Mannone and Nancy J. Flood

This index includes references to genera, species, authors, and key words or terms. In addition to avian species, references are made to the scientific names of all vertebrates mentioned within the volume and other taxa mentioned prominently in the text. Common names are as they appeared in the volume. Reference is made to books reviewed, reviewers, and announcements as they appeared in the volume.

Abburia spp., 246
Accipiter cooperii, 180, 213, 350, 353
  gentilis, 180
  striatus, 176–184, 350, 353
Acridotheres tristis, 463–476
Acrocephalus scirpaceus, 233
Actitis macularia, 208, 541, 544
Aegithina tiphia, 114–128
Aegolius acadicus, 554–555, 555–557
Agelaius phoeniceus, 89, 90–93, 93–95, 156–175, 215, 263, 265, 338, 372, 490, 550–554, 569–571, 589, 603
  xanthomus, 89–90
  xanthophthalmus, 490
Ahlquist, Jon E., see Sibley, Charles G. and ———
Aidley, D. J. (ed.), Animal migration, reviewed, 387–388
Aimophila aestivalis, 208–212
  ruficeps, 445
Aimophila spp., 433, 444, 445
Aix sponsa, 196
Akepa, see Loxops coccineus
Akiapolaau, see Hemignathus munroi
alarm calls
  response to by Calidris sandpipers, 322–328
Alauda arvensis, 463–476
Albatross, Black-footed, see Diomedea nigripes
Alca torda, 280
alewife, see Alosa pseudoharengus
Alopex lagopus, 370
Alosa aestivalis, 557–564
  pseudoharengus, 557–564, 575
Amakihi, Common, see Hemignathus virens
Amaurospiza concolor, 483
  moesta, 483
Amphispiza belli, 129–138
  bilineata, 546–550
Anas discors, 7
  platyrhynchos, 7, 196
  wyvilliana, 463–476
Anas sp., 7–8
Anatidae, 73
anatomy
  of hummingbirds, 71–73
Ancistrops strigilatus, 479
Anderson, Bertin W., see Meents, Julie K., ———, and Robert D. Ohmart
Anhinga spp., 366, 368
anhingas, see Anhinga spp.
Anhima cornuta, 478
Ankney, C. Davison and D. M. Scott, On the mating system of the Brown-headed Cowbirds, 260–268
announcements
  George Miksch Sutton (1898–1982), 476
  International Commission on Zoological Nomenclature, 19
  Laboratory of Ornithology magazine, 530
  Red-cockaded Woodpecker newsletter, 240
  Wilson Society committees, 104
Anodonta corpulenta, 84–85
Anous stolidus, 10
  stolidus ridgwayi, 10
Anser caerulescens, see Chen caerulescens
ant, harvest, see Pheidole sp.
ants, army, see Eciton burchelli, Eciton rapax, Labidus praedator
Antbird, Band-tailed, see Hypocnemoides maculicauda
  Bare-eyed, see Rhegmatorhina gymnops
  Black-chinned, see Hypocnemoides melanopogon
  Black-headed, see Percnostola rufifrons
  Chestnut-tailed, see Myrmeciza hemimelaena
  Crested, see Rhegmatorhina cristata

Ferruginous-backed, see Myrmeciza ferruginea
Goeldi's, see Myrmeciza goeldii
Long-tailed, see Drymophila caudata
Lunulated, see Gymnopithys lunulata
Ochre-rumped, see Drymophila ochropyga
Rufous-tailed, see Drymophila genei
Rufous-throated, see Gymnopithys rufigula
Salvin's, see Gymnopithys salvini
Scale-backed, see Hylophylax poecilinota
Silvered, see Scalteria naevia
Sooty, see Myrmeciza fortis
Spotted, see Hylophylax naevioides
Spot-backed, see Hylophylax naevia
Spot-winged, see Percnostola leucostigma devillei
Striated, see Drymophila devillei
Warbling, see Hypocnemis cantator
White-breasted, see Rhegmatorhina hoffmannsi
White-cheeked, see Gymnopithys leucaspis
White-lined, see Percnostola lophotes
White-plumed, see Pithys albifrons
White-shouldered, see Myrmeciza melanoceps
antbirds, see Formicariidae
antelope, pronghorn, see Antilocapra americana
Anthracothorax dominicus, 24, 30
Anthus pratensis, 233
spragueii, 51
Antilocapra americana, 192, 194
anting
by Agelaius xanthomus, 89–90
Antpitta, Bay-backed, see Grallaria hypoleuca
Black-crowned, see Pittasoma michleri
Chestnut-crowned, see Grallaria ruficapilla
Chestnut-napped, see Grallaria nuchalis
Hooded, see Grallaricula cucullata
Pale-billed, see Grallaria carrikeri (Frontispiece)
Rufous, see Grallaria rufula
Rufous-faced, see Grallaria erythrotis
Rusty-breasted, see Grallaricula ferrugineipectus
Rusty-tinged, see Grallaria przewalskii
Scaled, see Grallaria guatimalensis
Slate-crowned, see Grallaricula nana
Streak-chested, see Hylopezus perspicillatus
Tawny, see Grallaria quitensis atuensis
Undulated, see Grallaria squamigera
White-throated, see Grallaria albigula
Antshrike, Bluish-slate, see Thamnomanes schistogynus
Cinereous, see Thamnomanes caesius
Fasciated, see Cymbilaimus lineatus
Giant, see Batara cinerea
Spot-winged, see Pygiptila stellaris
antshrikes, see Thamnophilus spp., Sakesphorus spp.
Antthrush, Black-faced, see Formicarius analis
Short-tailed, see Chamaeza campanisona
Striated, see Chamaeza nobilis
Antwren, Ash-winged, see Terenura spodioptila
Chestnut-shouldered, see Terenura humeralis
Ihering's, see Myrmotherula iheringi
Ornate, see Myrmotherula ornata
Plain-throated, see Myrmotherula hauxwelli
Pygmy, see Myrmotherula brachyura
Rufous-bellied, see Myrmotherula guttata
Rufous-rumped, see Terenura callinota
Sclater's, see Myrmotherula sclateri
Streaked-capped, see Terenura maculata
White-eyed, see Myrmotherula leucophthalma
Yellow-rumped, see Terenura sharpei
Apapane, see Himatione sanguinea
Aphelocoma coerulescens, 604–606
Apherusa glacialis, 308
Apodidae, 73
Aquila chrysaetos, 34, 85, 180, 366
Aratinga holochlora brevipes, 11, 17
Archilochus alexandri, 546–550
Ardea cinerea, 575
herodias, 198–201, 204, 550–554, 571–577
herodias herodias, 571–577
Ardeidae, 73, 329
arrowweed, see Tessaria sericia
Artamidae, 114–128
Artamus spp., 114–128
Asio flammeus, 82–83, 463–476

Athene cunicularia, 9
Atriplex lentiformis, 583
Attila, Bright-rumped, see Attila spadiceus
Attila spadiceus, 456
Aulacorhynchus huallagae, 112
Auriparus flaviceps, 546–550, 583
Automolus melanopezus, 481
Avocet, American, see Recurvirostra americana
awards and grants
  Aaron M. Bagg student membership awards, 104, 432
  Frank M. Chapman Fund, 530
  Hawk Mountain research award, 239
  Louis Agassiz Fuertes award, 432
  Margaret Morse Nice award, 432
  Paul A. Stewart award, 432
  North American loon fund grants, 239
Aythya americana, 599–602
  ferina, 601–602
  valisineria, 599–602
Ball, Gregory, Barn Swallow fledgling successfully elicits feeding at a non-parental nest, 362–363
bamboo, see Guadua sp.
Bananaquit, see Coereba flaveola
Bancroft, G. Thomas and Glen E. Woolfenden, The molt of Scrub Jays and Blue Jays in Florida, reviewed, 604–606
Bancroft, Robert P., see Jamieson, Ian, Norman R. Seymour, and ———
Barclay, John H., see Sherrod, Steve K., William R. Heinrich, William A. Burnham, ———, and Tom J. Cade
Barlow, Jon C., see Orenstein, Ronald I. and ———
Barn-Owl, Common, see Tyto alba
Basileuterus culicivorus, 351, 352
Baskett, Thomas S., see Hardin, Kimberly I., ———, and Keith E. Evans
Batara cinerea, 483
Bayer, Range D., Great Blue Heron eggshell thickness at Oregon estuaries, 198–201
beaver, see Castor canadensis
Bednarz, James C. and James J. Dinsmore, Nest-site and habitat of Red-shouldered and Red-tailed hawks in Iowa, 31–45
beetle, southern pine, see Dendroctonus frontalis
behavior
  agonistic
    Charadrius vociferus, 515–530
    Parus atricapillus, 590–593
    Uria aalge, 595–598
  Alarm
    Hylophylax poecilinota, 449–451
  competitive
    Hylophylax poecilinota, 455–457
  courtship
    Charadrius melodus, 537–538
    Nyctea scandiaca, 79–81
  display
    Calamospiza melanocorys, 585–590
    Calcarus mccownii, 588–589
    Calcarus ornatus, 588
    Corapipo gutturalis, 594–595
  distraction
    Charadrius melodus, 539
    Parus atricapillus, 216–218
    Sitta carolinensis, 216–218
  food-related
    Pandion haliaetus, 557–564
    Sterna forsteri, 567–569
    Sterna hirundo, 567–569
  foraging, see foraging, behavior
  hunting
    Polyborus plancus, 565–566
  incubation
    Gavia immer, 361–362
  maintenance
    Hylophylax poecilinota, 458–460
    Pandion haeliaetus, 366–368
  nest provisioning
    by male Circus cyaneus, 564–565
  of the birds of southeastern Peru, 477–493
  parental
    Charadrius vociferus, 515–530
  reproductive
    Hylophylax poecilinota, 457–458
  sanitation, see nest, sanitation
  spatial
    Hylophylax poecilinota, 460–461
  territorial
    Charadrius melodus, 533–536
    Charadrius vociferus, 515–530
  vocal, see vocalizations
Beletsky, L. David, Vocal behavior of the Northern Oriole, 372–381
Bentz, Gregory Dean and Richard L. Zusi,

The humeroulnar pulley and its evolution in hummingbirds, 71–73
Berger, Andrew J., Hawaiian birdlife, 2nd ed., reviewed, 607
Berman, Susan L., review by, 386–387
Bernstein, Neil P., see Maxson Stephen J. and ———
Best, Loius B., see Stauffer, Dean F. and ———
birds of paradise, see Paradisaeidae
Bittern, American, see Botaurus lentiginosus
Blackbird, Pale-eyed, see Agelaius xanthophthalmus
Red-winged, see Agelaius phoeniceus
Yellow-headed, see Xanthocephalus xanthocephalus
Yellow-shouldered, see Agelaius xanthomus
Blackcap, see Sylvia atricapilla
Blair, Charles L. and Frank Schitoskey, Jr., Breeding biology and diet of the Ferruginous Hawk in South Dakota, 46–54
Blancher, Peter J. and Raleigh J. Robertson, A double-brooded Eastern Kingbird, 212–213
Bluebird, Eastern, see Sialia sialis
Fairy, see Irena puella
Mountain, see Sialia currucoides
bluebirds, see Sialia spp.
Bobolink, see Dolichonyx oryzivorus
Bock, Carl E., Factors influencing winter distribution and abundance of Townsend's Solitaire, 297–302
Bolin, Susan B., see Linz, George M. and ———
Bombycilla cedrorum, 602–603
Bombycilla spp., 301
Booby, Blue-footed, see Sula nebouxii
Brown, see Sula leucogaster
Masked, see Sula dactylatra
Red-footed, see Sula sula
Botaurus lentiginosus, 550–554
Boxall, Peter C. and M. Ross Lein, Possible courtship behavior by Snowy Owls in winter, 79–81
———, see McNicholl, Martin K., Philip H. R. Stepney, ———, and David A. E. Spalding
breeding biology, general
Accipiter cooperii, 213
birds of Kohala Mountain, Hawaii, 463–476
Buteo regalis, 46–54
Charadrius melodus, 531–545
Cistothorus platensis, 338–349
Jacana jacana, 206–208
Melospiza melodia, 584–585
Molothrus ater, 260–268
Pandion haliaetus, 557–564
Phalacrocorax auritus, 201–213
Tyrannus tyrannus, 212–213
Britton, P. L. (ed.), Birds of East Africa: their habitat, status and distribution, reviewed, 101–102
Britton, P. L., see Brown, L. H. and ———
Brodhead, Michael J., see Cutright, Paul R. and ———
Bronson, Michael T., see Leopold, A. Starker, Ralph J. Gutiérrez, and ———
Brown, L. H. and P. L. Britton, The breeding seasons of East African birds, reviewed, 101–102
Brown, R. G. B., see Orr, Craig D., Richard M. P. Ward, Norman A. Williams, and ———
Browne, Micou M., see Post, William and ———
Bubo virginianus, 156–175
Bubulcus ibis, 7, 565–566
Budgerigar, see Melopsittacus undulatus
Bullfinch, Puerto Rican, see Loxigilla portoricensis
Bunting, Indigo, see Passerina cyanea
Lark, see Calamospiza melanocorys
Snow, see Plectrophenax nivalis
Burger, J., B. L. Olla and H. E. Winn (eds.), Behavior of marine animals, current perspectives in research, Vol. 4, marine birds, reviewed, 390
Burnham, William A., see Sherrod, Steve K., William R. Heinrich, ———, John H. Barclay, and Tom J. Cade
Burns, Jeffrey T., Nests, territories, and reproduction of Sedge Wrens (Cistothorus platensis), 338–349
butcherbirds, see Cracticidae
Buteo jamaicensis, 4, 31–45, 176–184, 353
jamaicensis calurus, 8
jamaicensis socorroensis, 8

lagopus, 180
lineatus, 31–45, 180
lineatus alleni, 566–567
platypterus, 176–184, 350, 365–366
regalis, 46–54, 156
solitarius, 463–476
Butler, Robert W., Possible use of legs as dissipators of heat in flying Cliff Swallows, 87–89
Butorides striatus, 550–554
Cade, Tom J., see Sherrod, Steve K., William R. Heinrich, William A. Burham, John H. Barclay, and ———
Cairns, Winifred E., Biology and behavior of breeding Piping Plovers, 531–545
Calamospiza melanocorys, 51, 74–79, 96, 329–337
Calcarus mccownii, 585–590
ornatus, 50, 585–590
Calidris alba, 544
alpina, 322–328, 526
mauri, 9, 322–328
minutilla, 9, 322–328, 543
Calidris spp., 322–328
Cambarus sp., 85
Campephagidae, 114–128
Campephilus rubricollis, 451
Campylorhynchus brunneicapillus, 546–550, 582–584
Canary, see Serinus canaria
Cancer magister, 85
Canis latrans, 49
Cannell, Peter F., review by, 604–606
Canvasback, see Aythya valisineria
Caprimulgus carolinensis, 604, 610
vociferus, 604
Caracara, Crested, see Polyborus plancus
Cardinal, see Cardinalis cardinalis
Cardinalis cardinalis, 74–79, 210, 377, 463–476, 546–550
Carduelis tristis, 74–79, 160
Carpodacus mexicanus, 463–476
Caryothraustes canadensis, 491
humeralis, 491
Casiornis rufa, 487–488, 492
Cassiornis, Rufous, see Casiornis rufa
Castor canadensis, 322
cat, feral, see Felis catus
Catbird, Gray, see Dumetella carolinensis
catfish, channel, see Ictalurus punctatus
walking, see Clarias batrachus
Catharacta chilensis, 269
lonnbergi, 269
maccormicki, 269–281
skua, 269, 280
Cathartes aura, 214, 353
Catharus fuscescens, 489, 491, 492
minimus, 491
usulatus, 351, 491
Catoptrophorus semipalmatus, 326, 550–554
Catostomus commersonei, 557–564
cedar, salt, see Tamarix chinensis
Celeus spectabilis, 483
Censky, Ellen J. and Millicent S. Ficken, Responses of Black-capped Chickadees to mirrors, 590–593
census
birds on Kohala Mountain, Hawaii, 463–476
birds of prairie wetlands of South Dakota, 550–554
censusing methods
in desert riparian and scrub habitat, 546–550
Centrocercus urophasianus, 193, 194
Centurus uropygialis, 546–550
Cepphus columba, 356
grylle, 356–358
Cercophithecus aethiops, 322
Ceryle alycon, 12
chacalacas, see Ortalis spp.
Chaffinch, see Fringilla coelebs
Chamaepetes spp., 246
Chamaeza campanisona, 486
nobilis, 486
Chapman, Brian R., An apparent instance of communal nesting by American Oystercatchers, 584
Charadriidae, 73
Charadriiformes, 282
Charadrius alexandrinus, 87
alexandrinus alexandrinus, 531–545
alexandrinus nivosus, 538, 541
dubius, 531–545
hiaticula, 531–545
melodus, 531–545
montanus, 525–526, 531–545
ruficapillus, 532, 538, 539
semipalmatus, 9, 324, 536, 544
vociferus, 9, 85–87, 324, 326, 515–530, 531–545

wilsona, 532, 536, 538
Charadrius spp., 538
Chasiempis sandwichensis, 463–476
Chat, Yellow-breasted, see Icteria virens
Chat-Tyrant, Crowned, see Ochthoeca frontalis orientalis
Chauna torquata, 478, 492
Chen caerulescens, 318
caerulescens caerulescens, 494–504
rossii, 502
Chickadee, Black-capped, see Parus atricapillus
Boreal, see Parus hudsonicus
Carolina, see Parus carolinensis
chipmunk, eastern, see Tamias striatus
least, see Eutamias minimus
Chlidonias niger, 550–554
Chlorostilbon maugaeus, 27, 30
Chordeiles minor, 26
Chuck-will's-widow, see Caprimulgus carolinensis
Circus buffoni, 206
cyaneus, 180, 323, 564–565
Ciridops anna, 463
Cistothorus palustris, 338
platensis, 338–349
clams, see Lampsilis sp., Saxidormus spp., Tapes spp., Clinocardium spp.
Clancey, P. A. (ed.), SAOS checklist of southern African birds, reviewed, 380–391
Claravis godefrida, 483
mondetoura, 483
Clarias batrachus, 566
Clements, James F., Birds of the world: a checklist, 3rd ed., reviewed, 608–610
Clinocardium spp., 282–288
clutch-size
Agelaius phoeniceus, 569–571
Coccyzus americanus, 26
cinereus, 479, 492
cod, see Eleginus gracilis
Coereba flaveola, 23–25, 30
Coerebidae, 114–128
Coffey, Michael A., see Grubb, Teryl G. and ———
Colaptes auratus, 51, 74–79, 96, 329–337
Coleoptera, 135
Columba livia, 71, 468
Columbidae, 73
Columbina passerina, 23, 29
passerina socorroensis, 11, 17
Columbina spp., 8
competition
between Agelaius phoeniceus and Quiscalus quiscula, 90–93
Compsothlypidae, 114–128
Conner, Richard N. and Brian A. Locke, Fungi and Red-cockaded Woodpecker cavity trees, 64–70
Conopophaga aurita, 456
peruviana, 486–487
Contopus virens, 491
Coot, American, see Fulica americana
Coragyps atratus, 214
Corapipo gutturalis, 594–595
leucorrhoa, 595
Cormorant, Double-crested, see Phalacrocorax auritus
Olivaceous, see Phalacrocorax olivaceous
cormorants, see Phalacrocorax spp.
Cornely, John E., see Thompson, Steven P. and ———
Corvidae, 114–128
corvids, see Corvidae
Corvus brachyrhynchos, 74–79, 114–128, 156–175, 566–567
corax clarioensis, 12
moneduloides, 593
Corvus spp., 85, 542
cottontail, eastern, see Sylvilagus floridanus
Cowbird, Brown-headed, see Molothrus ater
Shiny, see Molothrus bonariensis
coyote, see Canis latrans
crab, see Cancer magister
Cracticidae, 114–128
Crane, Greater Sandhill, see Grus canadensis tabida
Sandhill, see Grus canadensis
Crawford, John A., review by, 607–608
Crax rubra, 246
Crax spp., 245
crayfish, see Cambarus sp.
Creeper, Hawaiian, see Oreomystis mana
Crow, American, see Corvus brachyrhynchos
New Caledonian, see Corvus moneduloides
crows, see Corvus spp.
Crypturellus soui, 490

Ctenosaur sp., 566
Cuckoo, Ash-colored, see Coccyzus cinereus
  Common, see Cuculus canorus
  Puerto Rican Lizard, see Saurothera vieilloti
  Yellow-billed, see Coccyzus americanus
Cuckoo-shrike, Large, see Coracina novaehollandiae
cuckoo-shrikes, see Campephagidae
Cuculus canorus, 233–235
curassow, see Nothocrax sp.
Curassow, Great, see Crax rubra
  Helmeted, see Pauxi [Crax] pauxi
Cutright, Paul R. and Michael J. Brodhead, Elliott Coues: naturalist and frontier historian, reviewed, 230–231
Cyanocitta cristata, 74–79, 156–175, 196, 593, 604–606
Cyanocorax morio, 565–566
  yncas, 593–594
Cyclarhidae, 114–128
Cyclarhis gujanensis, 114–128
Cyclarhis spp., 114–128
Cymbilaimus lineatus, 482
Cynomys ludovicianus, 50
Davis, Thomas H., A flight song display of White-throated Manakin, 594–595
DeCapita, Michael E., see Kelly, Sean T. and ———
Dendragapus obscurus, 590
Dendrocincla fuliginosa, 456
  merula, 451, 456
Dendroctonus frontalis, 64
Dendroica adelaidae, 30
  castanea, 15
  coronata, 15
  discolor, 25, 30, 210
  kirtlandii, 363–365
  pensylvanica, 14, 352, 353
  petechia, 15, 338, 546–550
  tigrina, 25, 30
  townsendi, 15, 352
  virens, 15, 352
Dicrurus paradiseus, 114–128
Dicrurus spp., 114–128
diet
  Amphispiza belli, 129–138
  Buteo regalis, 46–54
  Charadrius vociferus, 85–87
  Haliaeetus leucocephalus, 84–85
  Larus hyperboreus, 369–372
  Polyborus plancus, 565–566
  Rallus longirostris levipes, 215
Dinsmore, James J., see Bednarz, James C. and ———
Diomedea nigripes, 3
Dipodomys ordi, 50
Diptera, 368–369
distribution
  birds of southeastern Peru, 477–493
  summer
    Chen caerulescens caerulescens, 494–504
Divoky, George J., The occurrence and behavior of non-breeding Horned Puffins at Black Guillemot colonies in northern Alaska, 356–358
DNA-DNA hybridization
  Vireoninae, 114–128
Dolichonyx oryzivorus, 491
Donacobius atricapillus, 490
Doradito, Subtropical, see Pseudocolopteryx acutipennis
Dotterel, Red-capped, see Charadrius ruficapillus
Dove, Mourning, see Zenaida macroura
  Rock, see Columba livia
  Socorro, see Zenaida graysoni
  Spotted, see Streptopelia chinensis
  White-winged, see Zenaida asiatica
  Zebra, see Geopelia striata
  Zenaida, see Zenaida aurita
Dowitcher, Long-billed, see Limnodromus scolopaceus
dowitchers, see Limnodromus spp.
Dowler, Robert C., High mortality of Cedar Waxwings associated with highway plantings, 602–603
Drennan, Susan Roney, Where to find birds in New York state, reviewed, 610–611
Drepanidinae, 463–476
Drongo, Paradise, see Dicrurus paradiseus
drongos, see Dicrurus spp.
Dryocopus pileatus, 74–79
Drymophila caudata, 482–483
  devillei, 481, 482–483, 492
  genei, 483
  ochropyga, 483
Duck, Hawaiian, see Anas wyvilliana
  Wood, see Aix sponsa

duck, see Anas sp.
Duffin, K. E., review by, 235–236
Dumetella carolinensis, 74–79, 156–175, 215
Dunlin, see Calidris alpina
Dunn, Jon, see Garrett, Kimball and ———
Eagle, Bald, see Haliaeetus leucocephalus
Golden, see Aquila chrysaetos
Vulturine Fish, see Gyphoierax angolensis
Eaton, Stephen W., Birds of Cattaraugus County, New York, reviewed, 392
Eciton burchelli, 447–462
rapax, 447–462
Eckert, Allan W., The wading birds of North America (north of Mexico), reviewed, 388–390
ecological
release
of an insular avifauna, 139–155
separation
grebes and coots, 505–514
Edwards, Martin H., Ron D. Weir, and Robert B. Stewart, Comments on sexing Saw-whet Owls by wing chord, 555–557
eel, American, see Anguilla rostrata
eggshell thickness
Ardea herodias, 198–201
Egret, Cattle, see Bubulcus ibis
Great, see Egretta albus
Snowy, see Egretta thula
Egretta albus, 204
caerulea, 82, 215–216, 576
thula, 7
Elaenia, Caribbean, see Elaenia martinica
Mountain, see Elaenia frantzii
Yellow-bellied, see Elaenia flavogaster
Elaenia flavogaster, 114–128
frantzii, 351
martinica, 29
Elanoides forficatus, 353, 366
Elaphe vulpina, 217, 218
Elder, William H., see Norris, Douglas J. and ———
Eleagnus pungens, 602–603
Eleginus gracilis, 371–372
Elepaio, see Chasiempis sandwichensis
Eley, J. William, Systematic relationships and zoogeography of the White-winged Guan (Penelope albipennis) and related forms, 241–259
Elias, Donald J. and Danilo Valencia, Unusual feeding behavior by a population of Black Vultures, 214
Elowson-Haley, A. M., Osprey spreads wings after fishing, 366–368
Emerald, Puerto Rican, see Chlorostilbon maugaeus
Empidonax alnorum, 491
flavescens, 350
virescens, 449
Eremophila alpestris, 50
Esox lucius, 85
Eudocimus albus, 215, 216, 565
Euphonia, Blue-hooded, see Euphonia musica
Euphonia musica, 29
Eutamias minimus, 217, 218
Evans, Keith E., see Hardin, Kimberly I., Thomas S. Baskett, and ———
Faaborg, John, Avian population fluctuations during drought conditions in Puerto Rico, 20–30
Falco columbarius, 100–101, 180
peregrinus, 9, 180
sparverius, 180, 323
subbuteo, 100
Falcon, Laughing, see Herpetotheres cachinnans
Peregrine, see Falco peregrinus
Falconiformes, 73, 282
Falxa, Gary, see Whitacre, David, Devora Ukrain, and ———
faunal accounts
Revillagigedo Islands, Mexico, 1–19
Felis catus, 4
Ferguson, Howard L., see Jorgensen, Paul D. and ———
Fetterolf, Peter M., review by, 390
Ficken, Millicent S., Censky, Ellen J. and ———
Ficken, Millicent S., see Ficken, Robert W. and ———
Ficken, Robert W. and Millicent S. Ficken, Interspecific plumage similarity: the Mockingbird and Loggerhead Shrike, 223
Finch, Deborah M., Interspecific nest use by aridland birds, 582–584
Finch, House, see Carpodacus mexicanus
Saffron, see Sicalis flaveola

Slaty, see Haplospiza rustica
Uniform, see Haplospiza unicolor
Zapata, see Torreornis inexpectata
Zebra, see Poephila guttata
Flake, Lester D., see Weber, Michael J., Paul A. Vohs, Jr., and ———
Flatbill, Large-headed, see Ramphotrigon megacephala
Flicker, Common, see Colaptes auratus
flocking
Grus canadensis, 313–321
Florida caerulea, see Egretta caerulea
flounder, winter, see Pseudopleuronectes americanus
Flycatcher, Acadian, see Empidonax virescens
Alder, see Empidonax alnorum
Ash-throated, see Myiarchus cinerascens
Great Crested, see Myiarchus crinitus
Rusty-margined, see Myiozetetes cayanensis
Short-crested, see Myiarchus ferox
Stolid, see Myiarchus stolidus
Wied's Crested, see Myiarchus tyrannulus
Yellow-bellied, see Emphidonax flavescens
Foliage-gleaner, Brown-rumped, see Automolus melanopezus
Buff-browed, see Syndactyla rufosuperciliata
Lineated, see Syndactyla subalaris
foraging
behavior
Coragyps atratus, 214
Hydranassa caerulea, 215–216
Hylophylax poecilinota, 457–458
Larus atricilla, 223–225
of an insular avifauna, 139–155
Setophaga ruticilla, 289–296
Stelgidopteryx ruficollis, 368–369
success
Asio flammeus, 82–83
Forest-Falcon, Barred, see Micrastur ruficollis
Formicariidae, 105–113
Formicarius analis, 490
Formicidae, 135
fox, Arctic, see Alopex lagopus
red, see Vulpes fulva, Vulpes vulpes
Francolin, Black, see Francolinus francolinus
Erckel's, see Francolinus erckelii
Grey, see Francolinus pondicerianus
Francolinus erckelii, 469
francolinus, 469
pondicerianus, 469
Fratercula arctica, 140, 276, 280, 281
corniculata, 356–358
Fregata magnificens, 7
minor, 6–7
French, Thomas W., Piracy by a Great Black-backed Gull on a shark, 96
Frigatebird, Greater, see Fregata minor
Magnificent, see Fregata magnificens
Fringilla coelebs, 590
Fringillidae, 114–128
frog, green tree, see Hyla cinerea
leopard, see Rana pipiens
Fulica americana, 61, 85, 505–514
Fulmar, Southern Giant, see Macronectes giganteus
Funambulus pamarum, 218
Fundulus heteroclitus, 575
fungus, red heart, see Phellinus [Fomes] pini
Galliformes, 73
Gallinule, Azure, see Porphyrula flavirostris
Purple, see Porphyrula martinica
Gannet, Northern, see Sula bassanus
Gardner, Kenneth A., Birds of Oak Hammock Marsh Wildlife Management Area, reviewed, 391
Garrett, Kimball and Jon Dunn, Birds of southern California. Status and distribution, reviewed, 232–233
Garrulax canorus, 463–476
gaspereaux, see Alosa pseudoharengus
Gavia immer, 361–362
Gayou, Douglas C., Tool use by Green Jays, 593–594
Geococcyx californianus, 354–355, 582
Geopelia striata, 468
Geothlypis trichas, 114–128, 156–175, 338, 380, 594
Gessaman, James A. and Gary L. Worthen, The effect of weather on avian mortality, reviewed, 611
Glaucidium brasilianum, 479
minutissimum, 479–480

Glaucomys volans, 217, 218
Globicephala macrorhynca, 383
Gnatcatcher, Black-tailed, see Polioptila melanura
Blue-gray, see Polioptila caerulea
Gnateater, Ash-breasted, see Conopophaga peruviana
Chestnut-belted, see Conopophaga aurita
Godwit, Marbled, see Limosa fedoa
Goldfinch, American, see Carduelis tristis
Gonzalez Alonso, Hiram J., see Morton, Eugene S. and ———
Goose, Lesser Snow, see Chen caerulescens caerulescens
Ross', see Chen rossii
Snow, see Chen caerulescens
gopher, northern pocket, see Thomomys talpoides
Goshawk, see Accipiter gentilis
Grackle, Boat-tailed, see Quiscalus major
Common, see Quiscalus quiscula
Greater Antillean, see Quiscalus niger
Grallaria albigula, 111, 112
carrikeri, 105–113, 580–582 (Frontispiece)
erythrotis, 581
guatimalensis, 581
hypoleuca, 111
nuchalis, 105–113
nuchalis nuchalis, 108, 110
nuchalis obsoleta, 108
nuchalis ruficeps, 108
przewalskii, 109, 110, 112
quitensis atuensis, 112
ruficapilla, 109, 110, 112
rufula, 109
squamigera, 109, 110
Grallaria spp., 581
Grallaricula cucullata, 581
ferrugineipectus, 581
nana, 581
Grallaricula spp., 581
Grallina cyanoleuca, 114–128
Grant, Gibert S., see Pettit, Ted N., ———, and G. Causey Whittow
grasshopper, see Orthoptera
Grassquit, Black-faced, see Tiaris bicolor
Yellow-faced, see Tiaris olivacea
Gratson, Michael W., see Rosenfield, Robert N., Adam J. Rosenfield, and ———
Grebe, Eared, see Podiceps caspicus
Horned, see Podiceps auritus
Pied-billed, see Podilymbus podiceps
Greenlet, Dusky-capped, see Hylophilus hypoxanthus
Scrub, see Hylophilus flavipes
Tawny-crowned, see Hylophilus ochraceiceps
greenlets, see Hylophilus spp.
Grosbeak, Blue, see Guiraca caerulea
Evening, see Hesperiphona vespertina
Rose-breasted, see Pheucticus ludovicianus
Slate-colored, see Pitylus grossus
Yellow-green, see Caryothraustes canadensis
Yellow-shouldered, see Caryothraustes humeralis
Ground-Dove, Common, see Columbina passerina
Maroon-chested, see Claravis mondetoura
Purple-winged, see Claravis godefrida
ground-doves, see Columbina spp.
Grouse, Blue, see Dendragapus obscurus
Sage, see Centrocercus urophasianus
growth
Pterodroma hypoleuca, 358–361
Grubb, Teryl G. and Michael A. Coffey, Evidence of Bald Eagles feeding on freshwater mussels, 84–85
Grubb, Thomas C., Jr., Downy Woodpecker sexes select different cavity sites: an experiment using artificial snags, 577–579
Grus canadensis, 313–321
canadensis tabida, 313
Guadua sp., 477–493
Guan, Andean, see Penelope montagnii
Band-tailed, see Penelope argyrotis
Baudó, see Penelope ortoni
Bearded, see Penelope barbata
Cauca, see Penelope perspicax
Chestnut-bellied, see Penelope ochrogaster
Crested, see Penelope purpurascens
Dusky-legged, see Penelope obscura
Horned, see Oreophasis derbianus
Marail, see Penelope marail
Red-faced, see Penelope dabbenei

Rusty-margined, see Penelope superciliaris
Spix's, see Penelope jacquacu
White-browed, see Penelope jacucaca
White-crested, see Penelope pileata
White-winged, see Penelope albipennis
guans, see Arburria spp., Chamaepetes spp., Penelope spp., Penelopina spp., Pipile spp.
Guillemot, Black, see Cepphus grylle
Pigeon, see Cepphus columba
Guiraca caerulea, 210
Gull, California, see Larus californicus
Common Black-headed, see Larus ridibundus
Franklin's, see Larus pipixcan
Glaucous, see Larus hyperboreus
Glaucous-winged, see Larus glaucescens
Great Black-backed, see Larus marinus
Heermann's, see Larus heermanni
Laughing, see Larus atricilla
Lesser Black-backed, see Larus fuscus
Sabine's, see Xema sabini
Silver, see Larus novaehollandiae
Southern Black-backed, see Larus dominicanus
Western, see Larus occidentalis
gulls, see Larus spp.
Gutiérrez, Ralph J., see Leopold, A. Starker, ———, and Michael T. Bronson
Gymnopithys leucaspis, 455
lunulata, 451, 455
rufigula, 451, 456
salvini, 455
Gymnorhininae, 114–128
Gypohierax angolensis, 214
habitat
nesting
Aimophila aestivalis, 208–212
Buteo jamaicensis, 31–45
Buteo lineatus, 31–45
Haliaeetus leucocephalus, 55–63
of insular avifauna, 139–155
wintering
Amphispiza belli, 129–138
Hadden, Don, Birds of the North Solomons, reviewed, 231–232
Haematopus ostralegus, 541
palliatus, 584
Hailman, Jack P. and Jonathan R. Reed, Head wind promotes skimming in Laughing Gulls, 223–225
Halford, Douglas K., see Markham, O. Doyle and ———
Haliaeetus leucocephalus, 84–85, 180, 366
leucocephalus leucocephalus, 55–63
Haplospiza rustica, 483
unicolor, 483
Haramis, G. M., Records of Redhead × Canvasback hybrids, 599–602
Hardin, Kimberly I., Thomas S. Baskett, and Keith E. Evans, Habitat of Bachman's Sparrows breeding on Missouri glades, 208–212
Hardy, John William, Voices of New World nightbirds, Record #ARA–6, reviewed, 604
Harrier, Long-winged, see Circus buffoni
Northern, see Circus cyaneus
Hawk, Broad-winged, see Buteo platypterus
Cooper's, see Accipiter cooperii
Ferruginous, see Buteo regalis
Hawaiian, see Buteo solitarius
Red-shouldered, see Buteo lineatus
Red-tailed, see Buteo jamaicensis
Rough-legged, see Buteo lagopus
Sharp-shinned, see Accipiter striatus
Hawk-Eagle, Black, see Spizaetus tyrannus
Hays, Herbert E., see Reed, J. Michael, ———, and David A. Zegers
heat dissipation
Petrochelidon pyrronota, 87–89
Heinrich, William R., see Sherrod, Steve K., ———, William A. Burnham, John H. Barclay, and Tom J. Cade
Helmitheros vermivorus, 351, 353
Hemignathus lucidus, 463–476
munroi, 467
virens, 463–476
Hemiptera, 135
Hemispingus, Black-headed, see Hemispingus verticalis
Drab, see Hemispingus xanthophthalmus
Hemispingus verticalis, 111
xanthophthalmus, 111
Hemitriccus diops, 483
flammulatus, 483, 488
Heron, Great Blue, see Ardea herodias
Great White, see Ardea herodias
Green-backed, see Butorides striatus

Grey, see Ardea cinerea
Little Blue, see Egretta caerulea
heron, see Ardeidae
Herpetotheres cachinnans, 83–84
herring, blueback, see Alosa aestivalis
Hesperiphona vespertina, 301
Heterodon nasicus, 51
Him, Willie, review by, 390–391
Himatione sanguinea, 125, 463–476
Hirundo albigularis, 89
cucullata, 89
rustica, 160, 193, 194, 195, 223, 350, 362–363, 368, 491
Hobby, see Falco subbuteo
Homoptera, 135
honeycreepers, see Coerebidae
Honeyeater, Buff-breasted, see Meliphaga flaviventer
Hookbill, Chestnut-winged, see Ancistrops strigilatus
Hoplopterus armatus, 536
Howman, K. C. R., Pheasants, their breeding and management, reviewed, 392
human disturbance, effects of
Ardea herodias, 198–201
Dendroica kirtlandii, 363–365
Haliaeetus leucocephalus, 55–63
Zenaida macroura, 185–197
Hummingbird, Black-chinned, see Archilochus alexandri
hummingbirds, see Trochilidae
hybridization
Aythya americana × Aythya valisinneria, 599–602
Sialia sialis × Sialia currucoides, 219–223
Hydranassa caerulea, see Egretta caerulea
Hydrophasianus chirurgus, 206
Hyla cinerea, 86
Hylexetastes perrotti, 451, 456
Hylocichla mustelina, 351, 353
Hylopezus perspicillatus, 580–581
Hylophilus flavipes, 114–128
hypoxanthus, 483
ochraceiceps, 114–128
Hylophilus spp., 114–128, 483
Hylophylax naevia, 455
naevioides, 448, 455
poecilinota, 447–462
poecilinota duidae, 447
poecilinota nigrigula, 449
poecilinota poecilinota, 447
poecilinota vidua, 449
Hylophylax spp., 448
Hypocnemis cantator, 481, 490
Hypocnemoides maculicauda, 484
melanopogon, 484
Hypocnemoides spp., 448
Hypsibemon spp., 481
Ibis, White, see Eudocimus albus
Ictalurus punctatus, 85
Icteria virens, 125, 546–550
Icterus dominicensis, 30
galbula, 353
galbula galbula, 353, 372–381
icterus, 30
spurius, 89
Icterus spp., 372
Iguana sp., 566
Iiwi, see Vestiaria coccinea
Inezia inornata, 487, 489, 492
inkweed, see Suaeda torreyana
'io, see Buteo solitarius
Iora, Common, see Aegithina tiphia
Irena puella, 114–128
Jacana, Bronze-winged, see Hydrophasianus chirurgus
Northern, see Jacana spinosa
Wattled, see Jacana jacana
Jacana jacana, 206–208
spinosa, 206, 208
jackrabbit, white-tailed, see Lepus townsendii
Jackson, Jerome A., An annotated bibliography of the Red-cockaded Woodpecker, reviewed, 392
Jaeger, Parasitic, see Stercorarius parasiticus
Pomarine, see Stercorarius pomarinus
jaegers, see Stercorarius spp.
Jakle, Martin D., see Szaro, Robert C. and ———
James, Douglas, see Zammuto, Richard M. and ———
Jamieson, Ian, Norman R. Seymour, and Robert P. Bancroft, Use of two habitats related to changes in prey availability in a population of Ospreys in northeastern Nova Scotia, 557–564
Janovy, John, Yellowlegs, reviewed, 235–236
Jay, Blue, see Cyanocitta cristata

Brown, see Cyanocorax morio
Gray, see Perisoreus canadensis
Green, see Cyanocorax yncas
Scrub, see Aphelocoma coerulescens
Jehl, Joseph R., Jr., and Kenneth C. Parkes, The status of the avifauna of the Revillagigedo Islands, Mexico, 1–19
———, review by, 232–233
Jorgensen, Paul D. and Howard L. Ferguson, Clapper Rail preys on Savannah Sparrow, 215
Junco, Dark-eyed, see Junco hyemalis
Yellow-eyed, see Junco phaeonotus
Junco hyemalis, 140
phaeonotus, 326
Jungle-Babbler, Ferruginous, see Trichastoma bicolor
junipers, see Juniperus spp.
Juniperus spp., 297–302
Kelly, Sean T. and Michael E. DeCapita, Cowbird control and its effect on Kirtland's Warbler reproductive success, 363–365
Kemp, Thomas R., see Tramer, Elliot J. and ———
Kestrel, American, see Falco sparverius
Kilham, Lawrence, Florida Red-shouldered Hawk robs American Crows, 566–567
Killdeer, see Charadrius vociferus
King, A. S. and J. McLelland (eds.), Form and function in birds, Vol. 2, reviewed, 97
King, James R., see Mugaas, John N. and ———
Kingbird, Eastern, see Tyrannus tyrannus
Gray, see Tyrannus dominicensis
Western, see Tyrannus verticalis
Kingfisher, Belted, see Ceryle alcyon
Kinglet, Golden-crowned, see Regulus satrapa
kinglet, see Regulus sp.
Kirkpatrick, Charles M., see Lovvorn, James R. and ———
Kite, Swallow-tailed, see Elanoides forficatus
Kittiwake, Black-legged, see Rissa tridactyla
kleptoparasitism
by Buteo lineatus alleni on Corvus brachyrhynchos, 566–567
by Catharacta skua on Phalacrocorax atriceps, 269–281
by Larus marinus on sharks, 96
koloa, see Anas wyvilliana
Kress, Stephen W., The Audubon Society handbook for birders—a guide to locating, observing, identifying, recording, photographing and studying birds, reviewed, 237
Kushlan, James A. and Linda C. McEwan, Nesting phenology of the Double-crested Cormorant, 201–206
Labidus praedator, 447–462
Lagothrix flavicauda, 112
Lamna nasus, 96
Lamprospiza melanoleuca, 491
Lampsilis sp., 85
Laniidae, 114–128
Lanius collurio, 114–128
ludovicianus, 223
Lapwing, Northern, see Vanellus vanellus
Laridae, 73, 269
Lark, Horned, see Eremophila alpestris
Larus argentatus, 276, 280, 281
atricilla, 10, 223–225, 281, 368
californicus, 9
dominicanus, 276
fuscus, 280, 281
glaucescens, 10, 282–288, 590
heermanni, 9
hyperboreus, 369–372
marinus, 96
novaehollandiae, 281
occidentalis, 515
pipixcan, 10
ridibundus, 225, 527
Larus spp., 85, 269, 276, 542
Laughing-thrush, Melodius, see Garrulax canorus
LeFranc, Maurice N., Jr., Thomas A. Pierson, and Michael G. May, First record of a Bald Eagle nest in West Virginia, 366
Leger, Daniel W. and Jami L. Nelson, Effects of contextual information on behavior of Calidris sandpipers following alarm calls, 322–328
Lein, M. Ross, see Boxall, Peter C. and ———
Leiothrix, Red-billed, see Leiothrix lutea

Leiothrix lutea, 463–476
Lenington, Sarah and Rose Scola, Competition between Red-winged Blackbirds and Common Grackles, 90–93
Lentinus lepideus, 66
Lenzites saepiaria, 65
Leopold, A. Starker, Ralph J. Gutiérrez, and Michael T. Bronson, North American game birds and mammals, reviewed, 607–608
Lepus townsendii, 49, 50, 53
Limnodromus scolopaceus, 9
Limnodromus spp., 324, 326
Limosa fedoa, 326, 550–554
Linz, George M. and Susan B. Bolin, Incidence of Brown-headed Cowbird parasitism on Red-winged Blackbirds, 93–95
lizard, short-horned, see Phrynosoma douglassi
lizard, see Ctenosaur sp.
Lobipes lobatus, see Phalaropus lobatus
Locke, Brian A., see Conner, Richard N. and ———
Lonchura bicolor, 114–128
  malabarica, 468
  punctulata, 463–476
Long, Charles A., Comparison of the nest-site distraction displays of Black-capped Chickadee and White-breasted Nuthatch, 216–218
Longspur, Chestnut-collared, see Calcarus ornatus
  McCown's, see Calcarus mccownii
Loon, Common, see Gavia immer
Lophortyx gambelii, 546–550
Lophura leucomelana, 470
Lovvorn, James R. and Charles M. Kirkpatrick, Recruitment and socially-specific flocking tendencies of eastern Sandhill Cranes, 313–321
Loxigilla portoricensis, 23, 29
Loxops coccineus, 469
Lunda cirrhata, 356
Lustick, Sheldon, review by, 236
Lutra canadensis, 566
Machlolophus haplonotus, 218
Macronectes giganteus, 276
Mager, Doris, see Shapiro, Anne E., Frank Montalbano, III, and ———
Magpie, Black-billed, see Pica pica
Magpie-lark, Australian, see Grallina cyanoleuca
Mahoney, Shane P. and William Threlfall, Notes on the agonistic behavior of Common Murres, 595–598
Malaconotinae, 114–128
Mallard, see Anas platyrhynchos
management recommendations
  Kohala Mountain, Hawaii, 473–474
Manakin, White-ruffed, see Corapipo leucorrhoa
  white-throated, see Corapipo gutturalis
manatee, see Trichechus manatus
Mango, Antillean, see Anthracothorax dominicus
Mannikin, Bronze, see Lonchura bicolor
  Nutmeg, see Lonchura punctulata
Margarops fuscatus, 24, 29
Markham, O. Doyle and Douglas K. Halford, Radionuclides in Mourning Doves near a nuclear facility complex in southeastern Idaho, 185–197
marmot, hoary, see Marmota caligata
Marmota caligata, 322
Marr, Thomas G. and Douglas W. McWhirter, Differential hunting success in a group of Short-eared Owls, 82–83
Maxson, Stephen J. and Neil P. Bernstein, Kleptoparasitism by South Polar Skuas on Blue-eyed Shags in Antarctica, 269–281
May, Michael G., see LeFranc, Maurice N., Jr., Thomas A. Pierson, and ———
McEwan, Linda C., see Kushlan, James A. and ———
McIsaac, Hugh, review by, 387–388
McKitrick, Mary C., reviews by, 230–231, 238
McLaren, Margaret A., see McLaren, Peter L. and ———
McLaren, Peter L. and Margaret A. McLaren, Migration and summer distribution of Lesser Snow Geese in interior Keewatin, 494–504
McLelland, J., see King, A. S. and ———
McNabb, Roger A., review by, 388
McNicholl, Martin K. (ed.), Alberta naturalist, special issue no. 1, reviewed, 392

——— (ed.), Alberta naturalist, special issue no. 2, reviewed, 392
———, Philip H. R. Stepney, Peter C. Boxall, and David A. E. Spalding, A bibliography of Alberta ornithology, reviewed, 611
McWhirter, Douglas W., see Marr, Thomas G. and ———
Meadowlark, Eastern, see Sturnella magna
Western, see Sturnella neglecta
Meents, Julie K., Bertin W. Anderson, and Robert D. Ohmart, Vegetation relationships and food of Sage Sparrows wintering in honey mesquite habitat, 129–138
meetings and conferences
annual meeting, Raptor Research Foundation, 432
annual meeting, The Wilson Ornithological Society, 1983, 240, 432
behavior symposium, 239
birds and man: a symposium, 240
breeding birds in captivity symposium, 240
proceedings WOS annual meeting 1982, 612–623
XIX Congressus Internationalis Ornithologicus, 446
100th stated meeting of The American Ornithologists' Union, 1982, 239
sixth annual meeting of the Colonial Waterbird Group, 1982, 104
Tamaulipan Biotic Province symposium, 104
wildlife conference (raptors), 504
Melamprosops sp., 607
Melanerpes carolinus, 74–79, 329–337
erythrocephalus, 329–337
formicivorus, 297, 300
Meliphaga flaviventer, 114–128
Melopsittacus undulatus, 590
Melospiza georgiana, 140, 338
lincolnii,
melodia, 156–175, 584–585
Mengel, Robert M., review by, 604
Menidia menidia, 575
Merlin, see Falco columbarius
mesquite, honey, see Prosopis glandulosa
Metallura odomae, 111
theresiae, 111
Metaltail, Coppery, see Metallura theresiae
Neblina, see Metallura odomae
mice, see Peromyscus spp.
Micrastur ruficollis, 451
Micrathene whitneyi graysoni, 11, 17
Microtus longicaudus, 564
montanus, 564
oeconomus, 370
Microtus spp., 82
midges, see Diptera
migration
Chen caerulescens caerulescens, 494–504
of hawks, 176–184
Phalaropus fulicarius, 303–312
Phalaropus lobatus, 303–312
Mimocichla plumbea, 24, 29
Mimodes graysoni, 13, 16, 17 (Frontispiece)
Mimus gilvus, 223
patagonica, 223
polyglottos, 12–13, 14, 17, 29, 114–128, 223, 603
triurus, 223
Mitu spp., 245
Mniotilta varia, 25, 30, 351
Mock, Douglas W., review by, 388–390
Mockingbird, Northern, see Mimus polyglottos
Patagonia, see Mimus patagonica
Socorro, see Mimodes graysoni
Tropical, see Mimus gilvus
White-banded, see Mimus triurus
Mockingthrush, Black-capped, see Donacobius atricapillus
Molothrus ater, 93–95, 210, 260–268, 363–365, 372, 546–550, 584–585
ater obscurus, 582
bonariensis, 89
Monarch, Spot-winged, see Monarcha guttula
Monarcha guttula, 114–128
Monarcha spp., 114–128
Monarchidae, 114–128
monarchs, see Monarcha spp.
monkey, vervet, see Cercopithecus aethiops
yellow-tailed wooly, see Lagothrix flavicauda
Monore americana, 562
Monson, Gale and Allan R. Phillips, Annotated checklist of the birds of Arizona, 2nd ed., reviewed, 391
Montalbano, Frank, III, see Shapiro, Anne E., ———, and Doris Mager

Morse, Douglass H., Behavioral mechanisms in ecology, reviewed, 97–98
mortality
of Bombycilla cedrorum associated with highway plantings, 602–603
Morton, Eugene S. and Hiram J. Gonzalez Alonso, The biology of Torreornis inexpectata I. A comparison of vocalizations in T. i. inexpectata and T. i. sigmani, 433–446
Mosher, James A., see Titus, Kimberly and ———
Motacilla alba, 114–128
mouse, deer, see Peromyscus maniculatus
hispid pocket, see Perognathus hispidus
house, see Mus musculus
western harvest, see Reithrodontomys megalotis
white-footed, see Peromyscus leucopus
Mueller, Helmut C., Sexing Saw-whet Owls by wing chord, 554–555
Mugaas, John N. and James R. King, Annual variation of daily energy expenditure by the Black-billed Magpie: a study of thermal and behavioral energetics, reviewed, 236
mummichog, see Fundulus heteroclitus
Mundahl, John T., Role specialization in the parental and territorial behavior of the Killdeer, 515–530
Munro, Hugh L., see Rounds, Richard C. and ———
Murre, Common, see Uria aalge
murres, see Uria sp.
Mus musculus, 50
mussel, see Anodonta corpulenta
mussels, see Mytilus sp.
Mustela frenata, 50, 217, 218
Myadestes townsendi, 297–302
Myiarchus cinerascens, 546–550, 583
crinitus, 329–337
ferox, 487
stolidus, 24, 29
tyrannulus, 546–550
Myiozetetes cayanensis, 487, 492
Mynah, Common, see Acridotheres tristis
Myrmeciza ferruginea, 456
fortis, 455
goeldii, 485–486, 490, 492
hemimelaena, 490
melanoceps, 486
Myrmotherula brachyura, 482
guttata, 448
hauxwelli, 448
iheringi, 482, 492
leucophthalma, 482
ornata, 481, 482, 483
sclateri, 482
Mytilus sp., 85
Nectarinia jugularis, 114–128
Nelson, Colleen, A lamp-booth for laboratory use, 225–229
Nelson, Jami L., see Leger, Daniel W. and ———
Nero, Robert W., Post-copulatory display in the Lark Bunting and other species, 585–590
Nesospingus speculiferus, 89
nest
of Grallaria carrikeri, 580–582
of Grallariinae, 581
sanitation
Buteo platypterus, 365–366
nesting
Charadrius melodus, 539–542
communal
Haematopus palliatus, 584
interspecific
aridland birds in Arizona, 582, 584
success
Agelaius phoeniceus, 569–572
nestling
diet
Ardea herodias, 571–577
growth
Ardea herodias, 571–577
mortality
Ardea herodias, 571–577
nest-site
Buteo jamaicensis, 31–45
Buteo lineatus, 31–45
Haliaeetus leucocephalus, 366
Herpetotheres cachinnans, 83–84
in farmstead shelterbelts, 156–175
of cavity nesters in riparian habitats in Iowa, 329–337
Picoides borealis, 64–70
Tyrannus verticalis, 95–96
niche
segregation
by sex in Picoides pubescens, 577–579
Nighthawk, Common, see Chordeiles minor

Night-Heron, Black-crowned, see Nycticorax nycticorax
Yellow-crowned, see Nyctanassa violacea gravirostris
Noddy, Brown, see Anous stolidus
Norris, Douglas J. and William H. Elder, Decline of the Roadrunner in Missouri, 354–355
Nothocrax sp., 246
Notiochelidon cyanoleuca, 350
Nudds, Thomas D., Ecological separation of grebes and coots: interference competition or mirohabitat selection? 505–514
Nukupuu, see Hemignathus lucidus
Numenius phaeopus, 9
Nuthatch, White-breasted, see Sitta carolinensis
Nyctanassa violacea gravirostris, 7, 17
Nyctea scandiaca, 79–81
Nycticorax nycticorax, 550–554
Oceanodroma tethys, 4
Ochthoeca frontalis orientalis, 112
Ohmart, Robert D., see Meents, Julie K., Bertin W. Anderson, and ———
Old World orioles, see Oriolidae
Olla, B. L., see Burger, J., ———, and H. E. Winn
Olson, Storrs L. and David W. Steadman, The relationships of the Pedionomidae (Aves: Charadriiformes), reviewed, 238
Onesimus glacialis, 308
Oporornis agilis, 491, 492
formosus, 352, 353
Orenstein, Ronald I. and Jon C. Barlow, Variation in the jaw musculature of the avian family Vireonidae, reviewed, 238
———, review by, 606–607
Oreomystis mana, 463–476
Oreophasis derbianus, 246
Oriole, Black-cowled, see Icterus dominicensis
Northern, see Icterus galbula
Orchard, see Icterus spurius
Oriolidae, 114–128
Ornithion inerme, 488
Orr, Craig D., Richard M. P. Ward, Norman A. Williams, and R. G. B. Brown, Migration patterns of Red and Northern phalaropes in southwest Davis Strait and in the northern Labrador Sea, 303–312
Ortalis spp., 246
Orthoptera, 135, 566
Orton, D. A., The merlins of the Welsh marshes, reviewed, 100–101
Osborne, David R., Replacement nesting and polyandry in the Wattled Jacana, 206–208
Osprey, see Pandion haliaetus
otter, river, see Lutra canadensis
Ou, see Psittirostra psittacea
Ovenbird, see Seiurus aurocapillus
Owl, Burrowing, see Athene cunicularia
Elf, see Micrathene whitneyi graysoni
Great Horned, see Bubo virginianus
Saw-whet, see Aegolius acadicus
Short-eared, see Asio flammeus
Snowy, see Nyctea scandiaca
Oystercatcher, American, see Haematopus palliatus
European, see Haematopus ostralegus
Pachycephalidae, 114–128
Pachycephalinae, 114–128
Pandion haliaetus, 9, 180, 366–368, 557–564
Panurinae, 114–128
Paradisaeidae, 114–128
Parakeet, Green, see Aratinga holochlora brevipes
Painted, see Pyrrhura picta
Rock, see Pyrrhura rupicola
parasitism
by Molothrus ater on Agelaius phoeniceus, 93–95
by Molothrus ater on Dendroica kirtlandii, 363–365
Parker, Theodore A., III, Observations of some unusual rainforest and marsh birds in southeastern Peru, 477–493
Parkes, Kenneth C., reviews by, 98–100, 231–232, 608–610, 610–611
———, see Jehl, Joseph R., Jr., and ———
Parrot, White-bellied, see Pionites leucogaster
Partridge, Gray, see Perdix perdix
Parula, Northern, see Parula americana
Tropical, see Parula pitiayumi graysoni
Parula americana, 14, 25, 30, 140
pitiayumi graysoni, 14, 17

Parus atricapillus, 139–155, 160, 169, 216–218, 329–337, 590–593
carolinensis, 74–79, 217
hudsonicus, 139–155, 217
major, 114–128, 218
Parus spp., 14
Pasquier, Roger F. (ed.), Conservation of New World parrots, reviewed, 386–387
Passer domesticus, 114–128, 156–175, 329–337, 463–476, 590
Passerculus sandwichensis, 140
sandwichensis beldingi, 215
Passerella iliaca, 139–155, 378
Passeres, 114–128
Passeriformes, 73
Passerina cyanea, 25, 30, 156–175, 353, 377, 380, 566, 590
Pauxi [Crax] pauxi, 246
Payne, Robert B., review by, 233–235
Pelecanus occidentalis, 82, 198
Pelican, Brown, see Pelecanus occidentalis
Penelope albipennis, 241–259 (Frontispiece)
argyrotis, 241
barbata, 241
dabbenei, 241, 242
jacquacu, 241–259 (Frontispiece)
jacucaca, 241
marail, 241, 247
montagnii, 241
obscura, 241–259
obscura bridgesi, 245
ochrogaster, 241
ortoni, 241, 242–243, 246–247
perspicax, 241–259
pielata, 241
purpurascens, 241–259 (Frontispiece)
superciliaris, 241, 247
Penelope spp., 241–259
Penelopina spp., 246
Penguin, Adélie, see Pygoscelis adelinae
Peppershrike, Rufous-browed, see Cyclarhis gujanensis
peppershrikes, see Cyclarhis spp.
Perca flavescens, 85, 562, 575
perch, white, see Monore americana
yellow, see Perca flavescens
Percnostola leucostigma, 485
lophotes, 484–485, 492
macrolopha, 484
rufifrons, 450, 456, 458, 460, 462, 485
Perdix perdix, 50
Perisoreus canadensis, 610
Perognathus hispidus, 50
Peromyscus leucopus, 217, 218
maniculatus, 50, 194
Peromyscus spp., 50
Petrel, Bonin, see Pterodroma hypoleuca
Dark-rumped, see Pterodroma phaeopygia
Petrochelidon pyrrhonota, 87–89
Pettit, Ted N., Gilbert S. Grant, and G. Causey Whittow, Body temperature and growth of Bonin Petrel chicks, 358–361
Pewee, Eastern Wood, see Contopus virens
Phaeolus schweinitzii, 65, 66
Phaeornis obscurus, 469, 473–474
Phaethon aethereus, 5
Phalacrocorax atriceps, 269–281
auritus, 96
olivaceous, 82
Phalacrocorax spp., 366, 368
Phalarope, Northern, see Phalaropus lobatus
Red, see Phalaropus fulicarius
Wilson's, see Phalaropus tricolor
Phalaropus fulicarius, 303–312
lobatus, 9, 303–312
tricolor, 550–554
Phasianus colchicus, 156, 160, 469
versicolor, 469
Pheasant, Blue, see Phasianus versicolor
Kalij, see Lophura leucomelana
Ring-necked, see Phasianus colchicus
Pheidole sp., 89
Phellinus [Fomes] pini, 64–70
Pheucticus ludovicianus, 353
Phlebia radiata, 66
Phrynosoma douglassi, 51
Pica pica, 114–128
pica hudsonia, 236
Picidae, 329, 582–584
Picoides borealis, 64–70
pubescens, 74–79, 160, 169, 329–337, 577–579
scalaris, 546–550
tridactylus, 610
Piculus simplex, 608
Pied-Tanager, Red-billed, see Lamprospiza melanoleuca
Pierson, Thomas A., see LeFranc, Maurice N., Jr., ———, and Michael G. May

pike, northern, see Esox lucius
pine, loblolly, see Pinus taeda
longleaf, see Pinus palustris
shortleaf, see Pinus echinata
Pinkowski, Benedict C., Western Kingbird nests in abandoned woodpecker cavity, 95–96
Pinus echinata, 64–70
palustris, 64–70
taeda, 64–70
Pionites leucogaster, 479, 490
Pipile spp., 241, 246
Pipilo aberti, 546–550, 582–584
erythrophthalmus, 74–79, 380
erythrophthalmus socorroensis, 15–16, 17
Pipilo sp., 445
Pipit, Meadow, see Anthus pratensis
Sprague's, see Anthus spragueii
Piranga ludoviciana, 353
olivacea, 491
rubra, 353, 546–550
Pithya albifrons, 455–456
Pittasoma michleri, 581
Pituophis melanoleucus, 51
Pitylus grossus, 490
Plectrophenax nivalis, 525
Plethodon cinereus, 525
Ploceus capensis, 114–128
Plover, Black-bellied, see Pluvialis squatarola
Blacksmith, see Hoplopterus armatus
Golden, see Pluvialis dominica
Kentish, see Charadrius alexandrinus alexandrinus
Little Ringed, see Charadrius dubius
Mountain, see Charadrius montanus
Piping, see Charadrius melodus
Ringed, see Charadrius hiaticula
Semipalmated, see Charadrius semipalmatus
Snowy, see Charadrius alexandrinus
Wilson's, see Charadrius wilsona
plumage
interspecific similarity between Mimus polyglottos and Lanius ludovicianus, 223
lamp-booth for laboratory study of, 225–229
Pluvialis dominica, 9, 87
squatarola, 9, 87
Pochard, Common, see Aythya ferina
Podiceps auritus, 505–514
caspicus, 505
Podilymbus podiceps, 3, 505–514
Poecilotriccus albifacies, 488
Poephila guttata, 590
Polioptila caerulea, 210
melanura, 583
Pollachius virens, 96, 575
pollock, see Pollachius virens
polyandry
Jacana jacana, 206–208
Polyborus plancus, 565–566
Pooecetes gramineus, 160
population dynamics
Geococcyx californianus, 354–355
West Indian avifauna, 20–30
porbeagle, see Lamna nasus
Porphyrula flavirostris, 478–479, 492
martinica, 478
Porzana carolina, 550–554
Post, William and Micou M. Browne, Active anting by the Yellow-shouldered Blackbird, 89–90
Powell, James A., see Scott, Michael D. and ———
prairie dog, black-tailed, see Cynomys ludovicianus
President's message
includes winners of the Louis Agassiz Fuertes award, 1947–1982, 430–431
Procellariidae, 73
Prosopis glandulosa, 129–138, 582–584
Protonotaria citrea, 25, 30
Pseudocolopteryx acutipennis, 488, 492
Pseudopleuronectes americanus, 557–564
Psittirostra psittacea, 463
Pterodroma hypoleuca, 358–361
phaeopygia, 359, 361
Pterodroma spp., 360
pueo, see Asio flammeus
Puffin, Common, see Fratercula arctica
Horned, see Fratercula corniculata
Tufted, see Lunda cirrhata
Puffinus auricularis, 1–4
creatopus, 3
diomedea, 381–385
diomedea borealis, 381, 383, 384
diomedea diomedea, 381, 383
gravis, 383

lherminieri, 381, 383
pacificus, 3
puffinus, 381
puffinus newelli, 470
Pulich, Warren, Jr., Documentation and status of Cory's Shearwater in the Western Gulf of Mexico, 381–385
Pygiptila stellaris, 479
Pygmy-Owl, Ferruginous, see Glaucidium brasilianum
Least, see Glaucidium minutissimum
Pygmy-Tyrant, Drab-breasted, see Hemitriccus diops
Flammulated, see Hemitriccus flammulatus
Pygoscelis adeliae, 82, 269, 597
Pyrrhura picta, 479
rupicola, 479
Quail, Gambel's, see Lophortyx gambelii
Quinney, T. E., Growth, diet, and mortality of nestling Great Blue Herons, 571–577
Quiscalus major, 610
niger, 89
quiscula, 90–93, 156–175, 372
Raikow, Robert J., reviews by, 97, 101, 102, 238, 391, 392, 607, 611
Rail, Clapper, see Rallus longirostris levipes
King, see Rallus elegans
Rallidae, 73
Rallus elegans, 215
longirostris levipes, 215
Ramphotrigon megacephala, 483, 492
Rana pipiens, 51
rat, Ord kangaroo, see Dopodomys ordi
Raven, Common, see Corvus corax clarionensis
Razorbill, see Alca torda
recruitment
Grus canadensis, 313–321
Recurvebill, Peruvian, see Simoxenops ucayalae
Recurvirostra americana, 322–328, 550–554
Redhead, see Aythya americana
Redstart, American, see Setophaga ruticilla
Reed, J. Michael, Herbert E. Hays, and David A. Zegers, Feeding behaviors and efficiencies of Common and Forster's terns, 567–569
Reed, Jonathan R., see Hailman, Jack P. and ———
Regulus satrapa, 140
Regulus sp., 489
Reithrodontomys megalotis, 50
Rhegmatorhina cristata, 455
gymnops, 451
hoffmannsi, 455
Rice, Jake C., see Vassallo, Monique I. and ———
Rigby, Michael D., Clutch-size and prefledging survival in Red-winged Blackbirds at Williamstown Lake, New Brunswick, 569–571
Riparia riparia, 266, 363, 491
Rissa tridactyla, 280, 281
Roadrunner, see Geococcyx californianus
Robbins, G. E. S., Quail, their breeding and management, reviewed, 392
Robbins, Mark B. and David A. Wiedenfeld, Observations at a Laughing Falcon nest, 83–84
Robertson, Raleigh Jr., see Blancher, Peter J. and ———
Robin, American, see Turdus migratorius
Mountain, see Turdus plebejus
White-throated, see Turdus albicollis
Rockwell, Elizabeth Drexler, Intraspecific food robbing in Glaucous-winged Gulls, 282–288
Rosenfield, Adam J., see Rosenfield, Robert N., ———, and Michael W. Gratson
Rosenfield, Robert N., Adam J. Rosenfield, and Michael W. Gratson, Unusual nest sanitation by a Broad-winged Hawk, 365–366
——— and Jonathan Wilde, Male Cooper's Hawk breeds in juvenal plumage, 213
Rounds, Richard C. and Hugh L. Munro, A review of hybridization between Sialia sialis and S. currucoides, 219–223
Rynchops niger, 223, 225, 515, 584
Sakesphorus spp., 485
salamander, red-backed, see Plethodon cinereus
Salmo gairdneri, 85
Salpinctes obsoletus exsul, 12
saltbush, see Atriplex lentiformis
Sanderling, see Calidris alba

Sandpiper, Semipalmated, see Calidris pusilla
Spotted, see Actitis macularia
Western, see Calidris mauri
Sapsucker, Yellow-bellied, see Sphyrapicus varius
Satrapa icterophrys, 487, 492
Saurothera vieilloti, 29
Saxicola rubetra, 101
Saxidomus spp., 282–288
Schardien, Bette J. and Jerome A. Jackson, Killdeers feeding on frogs, 85–87
Schitoskey, Frank, Jr., see Blair, Charles L. and ———
Schulenberg, Thomas S. and Morris D. Williams, A new species of antpitta (Grallaria) from northern Peru, 105–113
Sciurus carolinensis, 216–218
Sciurus sp., 451
Sclateria naevia, 484
Scola, Rose, see Lenington, Sarah and ———
Scott, D. M., see Ankney, C. Davison and ———
Scott, Michael D. and James A. Powell, Commensal feeding of Little Blue Herons with manatees, 215–216
Screamer, Horned, see Anhima cornuta
Southern, see Chauna torquata
Sealy, Spencer G., Rough-winged Swallows scavenging adult midges, 368–369
Seedeater, Blackish-blue, see Amaurospiza moesta
Blue, see Amaurospiza concolor
Slate-colored, see Sporophila schistacea
Temminck's, see Sporophila falcirostris
Seidel, George E. and Robert C. Whitmore, Effect of forest structure on American Redstart foraging behavior, 289–296
Seiurus aurocapillus, 25, 30, 352, 353
motacilla, 352, 353
noveboracensis, 25, 30, 139–155, 352
Serinus canaria, 380
Setophaga ruticilla, 14, 15, 24, 25, 30, 289–296, 353
sexing
Aegolius acadicus by wing chord, 554–555, 555–557
Seymour, Norman R., see Jamieson, Ian, ———, and Robert P. Bancroft
Shag, Blue-eyed, see Phalacrocorax atriceps
Shapiro, Anne E., Frank Montalbano, III, and Doris Mager, Implications of construction of a flood control project upon Bald Eagle nesting activity, 55–63
shark, mackerel, see Lamna nasus
Shearwater, Audubon's, see Puffinus lherminieri
Cory's, see Puffinus diomedea
Greater, see Puffinus gravis
Manx, see Puffinus puffinus
Pink-footed, see Puffinus creatopus
Townsend's, see Puffinus auricularis
Wedge-tailed, see Puffinus pacificus
Sherrod, Steve, review by, 100–101
———, William R. Heinrich, William A. Burnham, John H. Barclay, and Tom J. Cade, Hacking: a method for releasing Peregrine Falcons and other birds of prey, reviewed, 101
Shrike, Loggerhead, see Lanius ludovicianus
Red-backed, see Lanius collurio
shrikes, see Laniidae
Shrike-Vireo, Chestnut-sided, see Vireolanius melitophrys
shrike-vireos, see Vireolanius spp.
Shrubsall, Dennis (ed.), Birds of a feather: unpublished letters of W. H. Hudson, reviewed, 238
Sialia currucoides, 219–223, 300
sialis, 219–223, 333, 525
Sialia spp., 300, 301
Sibley, Charles G. and Jon E. Ahlquist, The relationships of the vireos (Vireoninae) as indicated by DNA-DNA hybridization, 114–128
Sicalis flaveola, 468
silverberry, see Eleagnus pungens
Silverbill, Warbling, see Lonchura malabarica
silverside, Atlantic, see Menidia menidia
Simoxenops ucayalae, 480–481, 483, 492
Sitta carolinensis, 74–79, 216–218, 329–337
Skadhauge, Erik, Osmoregulation in birds, reviewed, 388
Skimmer, Black, see Rynchops niger
Skua, Brown, see Catharacta lonnbergi
Chilean, see Catharacta chilensis
Great, see Catharacta skua

South Polar, see Catharacta maccormicki
Skutch, Alexander F., New studies of tropical American birds, reviewed, 608
Skylark, Eurasian, see Alauda arvensis
Smith, James N. M., review by, 97–98
———, Song Sparrow pair raise four broods in one year, 584–585
snake, fox, see Elaphe vulpina
gopher, see Pituophis melanoleucus
western hog-nosed, see Heterodon nasicus
Softtail, Russet-mantled, see Thripophaga berlepschi
Solitaire, Townsend's, see Myadestes townsendi
Sora, see Porzana carolina
Spalding, David A. E., see McNicholl, Martin K., Philip H. R. Stepney, Peter C. Boxall, and ———
Sparrow, Bachman's, see Aimophila aestivalis
Black-throated, see Amphispiza bilineata
Chipping, see Spizella passerina
Field, see Spizella pusilla
Fox, see Passerella iliaca
House, see Passer domesticus
Lincoln's, see Melospiza lincolnii
Rufous-crowned, see Aimophila ruficeps
Sage, see Amphispiza belli
Savannah, see Passerculus sandwichensis
Song, see Melospiza melodia
Swamp, see Melospiza georgiana
Vesper, see Pooecetes gramineus
White-throated, see Zonotrichia albicollis
sparrows, see Aimophila spp.
Spermophilus beecheyi, 322
tridecemlineatus, 49, 50, 53
Spermophilus sp., 564
Spheniscidae, 73
Sphyrapicus varius, 350
Spindalis zena, 27, 29
Spinetail, Pale-breasted, see Synallaxis albescens
Spizaetus tyrannus, 490
Spizella passerina, 156–175
pusilla, 210, 211
Sporophila falcirostris, 483
schistacea, 483, 491–492
squirrel, California ground, see Spermophilus beecheyi
gray, see Sciurus carolinensis
palm, see Funambulus palmarum
red, see Tamiasciurus hudsonicus
southern flying, see Glaucomys volans
thirteen-lined ground, see Spermophilus tridecemlineatus
squirrel, see Sciurus sp.
squirrels, ground, see Spermophilus sp.
Starling, Common, see Sturnus vulgaris
status
Puffinus diomedea, 381–385
Stauffer, Dean F. and Louis B. Best, Nest-site selection by cavity-nesting birds of riparian habitats in Iowa, 329–337
Steadman, David W., see Olson, Storrs L. and ———
Stelgidopteryx ruficollis, 12, 350, 353, 368–369
Stepney, Philip H. R., see McNicholl, Martin K., ———, Peter C. Boxall, and David A. E. Spalding
Stercorariidae, 269
Stercorarius parasiticus, 276, 280
pomarinus, 9
Stercorarius spp., 269, 276
Sterna bengalensis, 281
bergii, 281, 567
forsteri, 567–569
fuscata, 10, 381
hirundo, 280, 281, 567–569
maximus, 567
paradisaea, 280, 281
sandvicensis, 82, 280, 567
vittata, 276
Stewart, Robert B., see Edwards, Martin H., Ron D. Weir, and ———
Stiles, F. Gary, review by, 608
Storm-Petrel, Galapagos, see Oceanodroma tethys
Strang, Carl, Diet of Glaucous Gulls in western Alaska, 369–372
Streptopelia chinensis, 468
Sturnella magna, 169, 372
neglecta, 49, 50, 53, 372, 378
Sturnidae, 114–128
Sturnus vulgaris, 114–128, 156–175, 329–337
Suaeda torreyana, 129–138, 583
sucker, white, see Catostomus commersonei
Sula bassanus, 275, 280, 390
dactylatra, 5–6

leucogaster, 5, 6, 381
nebouxii, 5
sula, 5, 6
Sulidae, 73
Sunbird, Olive-backed, see Nectarinia jugularis
Sutcliffe, Scott, Prolonged incubation behavior in Common Loons, 361–362
Swallow, Bank, see Riparia riparia
Barn, see Hirundo rustica
Blue-and-white, see Notiochelidon cyanoleuca
Cliff, see Petrochelidon pyrrhonota
Larger Striped, see Hirundo cucullata
Rough-winged, see Stelgidopteryx ruficollis
White-throated, see Hirundo albigularis
swifts, see Apodidae
Sylvia atricapilla, 114–128
Sylviidae, 114–128
Sylvilagus floridanus, 50
Sylvioidea, 114–128
Synallaxis albescens, 480, 492
albescens australis, 480
Syndactyla rufosuperciliata, 480, 483
subalaris, 480
systematics
Grallaria, 105–113
Penelope albipennis, 241–259
Vireoninae, 114–128
Szaro, Robert C. and Martin D. Jakle, Comparison of variable circular-plot and spot-map methods in desert riparian and scrub habitats, 546–550
Tachyphonus cristatus, 491
rufiventer, 491
Tamarix chinensis, 583
Tamiasciurus hudsonicus, 170, 216–218
Tanager, Flame-crested, see Tachyphonus cristatus
Puerto Rican, see Nesospingus speculiferus
Scarlet, see Piranga olivacea
Stripe-headed, see Spindalis zena
Summer, see Piranga rubra
Western, see Piranga ludoviciana
Yellow-crested, see Tachyphonus rufiventer
Tapes spp., 282–288
taxonomy
birds of southeastern Peru, 477–493
Hylophylax poecilinota, 447–448
Teal, Blue-winged, see Anas discors
Terenura callinota, 484
humeralis, 483–484
maculata, 484
sharpei, 484
spodioptila, 484
Tern, Antarctic, see Sterna vittata
Arctic, see Sterna paradisaea
Black, see Chlidonias niger
Common, see Sterna hirundo
Crested, see Sterna bergii
Forster's, see Sterna forsteri
Lesser Crested, see Sterna bengalensis
Royal, see Sterna maximus
Sandwich, see Sterna sandvicensis
Sooty, see Sterna fuscata
Tessaria sericia, 583
Thamnomanes caesius, 486
schistogynus, 486
Thamnophilus spp., 485
Thomomys talpoides, 50
Thompson, Steven P. and John E. Cornely, Nest provisioning behavior of a male Northern Harrier on the death of his mate, 564–565
Thrasher, Brown, see Toxostoma rufum
Crissal, see Toxostoma dorsale
Pearly-eyed, see Margarops fuscatus
Threlfall, William, see Mahoney, Shane P. and ———
Thripadectes flammulatus, 111
scrutator, 111
Thripophaga berlepschi, 112
Thrush, Creamy-bellied, see Turdus amaurochalinus
Gray-cheeked, see Catharus minimus
Hawaiian, see Phaeornis obscurus
Lawrence's, see Turdus lawrencii
Red-legged, see Mimocichla plumbea
Swainson's, see Catharus ustulatus
Wood, see Hylocichla mustelina
Thryomanes sissonii, 12, 17
Thryothorus guarayanus, 489
leucotis, 489
leucotis peruanus, 489
ludovicianus, 74–79
Tiaris bicolor, 24, 29
olivacea, 29

Timaliidae, 114–128
Timalioidea, 114–128
Tinamidae, 73
Tinamou, Little, see Crypturellus soui
Tit, Great, see Parus major
tits, see Parus spp.
Titus, Kimberly and James A. Mosher, The influence of seasonality and selected weather variables on autumn migration of three species of hawks through the central Appalachians, 176–184
Todus mexicanus, 24, 29
Tody, Puerto Rican, see Todus mexicanus
Tody-Flycatcher, White-cheeked, see Poecilotriccus albifacies
tool use
  by Cyanocorax yncas, 593–594
Torreornis inexpectata, 433–446 (Frontispiece)
  inexpectata inexpectata, 433–446
  inexpectata sigmani, 433–446
  inexpectata varonai, 433, 444
Toucanet, Yellow-browed, see Aulacorhynchus huallagae
Towhee, Abert's, see Pipilo aberti
  Rufous-sided, see Pipilo erythrophthalmus
towhees, see Pipilo sp.
Toxostoma dorsale, 582–584
  rufum, 78, 156–175
Tramer, Elliot J. and Thomas R. Kemp, Notes on migrants wintering at Monteverde, Costa Rica, 350–354
Traylor, Melvin A., Jr., review by, 101–102
Treehunter, Buff-throated, see Thripadectes scrutator
  Flammulated, see Thripadectes flammulatus
Trichastoma bicolor, 114–128
Trichechus manatus, 215–216
Tringa flavipes, 550–554
  melanoleucus, 544
Trochilidae, 71–73
Troglodytes aedon, 114–128, 217, 329–337
  tanneri, 12
Tropicbird, Red-billed, see Phaethon aethereus
Troupial, see Icterus icterus
trout, rainbow, see Salmo gairdneri
Turdus albicollis, 351
  amaurochalinus, 489–490, 492
  lawrencii, 490
  migratorius, 74–79, 114–128, 156–175, 300, 301
  plebejus, 351
Tyrannulet, Plain, see Inezia inornata
  White-lored, see Ornithion inerme
Tyrannus dominicensis, 29
  tyrannus, 95, 156–175, 212–213, 491
  verticalis, 95–96
Tyrant, Yellow-browed, see Satrapa icterophrys
Tyto alba, 4, 11, 468
Ukrain, Devora, see Whitacre, David, ———, and Gary Falxa
Ula-ai-hawane, see Ciridops anna
Uria aalge, 280, 595–598
Uria sp., 358
Valencia, Danilo, see Elias, Donald J. and ———
van Riper, Charles, III, Censuses and breeding observations of the birds on Kohala Mountain, Hawaii, 463–476
Van Tyne Memorial Library list, 393–429
Vanellus vanellus, 527, 532
vanga shrikes, see Vangidae
Vangidae, 114–128
Vassallo, Monique I. and Jake C. Rice, Ecological release and ecological flexibility in habitat use and foraging of an insular avifauna, 139–155
Veery, see Catharus fuscescens
Verdin, see Auriparus flaviceps
Vermivora celata, 14
  chrysoptera, 352
  luciae, 546–550
  peregrina, 14, 351, 352
Vermivora sp., 489
Vestiaria coccinea, 463–476
Vireo, Bell's, see Vireo bellii
  Black-whiskered, see Vireo altiloquus
  Brown-capped, see Vireo gilvus leucophrys
  Philadelphia, see Vireo philadelphicus
  Puerto Rican, see Vireo latimeri
  Red-eyed, see Vireo olivaceus
  Solitary, see Vireo solitarius
  White-eyed, see Vireo griseus
  Yellow-throated, see Vireo flavifrons
Vireo altiloquus, 26, 114–128

bellii, 546–550
flavifrons, 351
gilvus leucophrys, 351
griseus, 74–79, 114–128
latimeri, 24, 30
olivaceus, 114–128
philadelphicus, 351
solitarius, 114–128, 351
Vireo spp., 114–128
Vireolaniidae, 114–128
Vireolaniinae, 114–128
Vireolanius melitophrys, 118
Vireolanius spp., 114–128
Vireoninae, 114–128
vocalizations
Hylophylax poecilinota, 448–449
Icterus galbula galbula, 372–381
morning onset in an Ozark community, 74–79
Torreornis inexpectata inexpectata, 433–446
Torreornis inexpectata sigmani, 433–446
Vohs, Paul A., Jr., see Weber, Michael J., ———, and Lester D. Flake
vole, long-tailed, see Microtus longicaudus
montane, see Microtus montanus
tundra, see Microtus oeconomus
voles, see Microtus spp.
Vulpex fulva, 49
vulpes, 370
Vulture, Black, see Coragyps atratus
Palm Nut, see Gypohierax angolensis
Turkey, see Cathartes aura
Wagtail, White, see Motacilla alba
Warbler, Adelaide's, see Dendroica adelaidae
Bay-breasted, see Dendroica castanea
Black-and-white, see Mniotilta varia
Black-throated Green, see Dendroica virens
Canada, see Wilsonia canadensis
Cape May, see Dendroica tigrina
Chestnut-sided, see Dendroica pensylvanica
Connecticut, see Oporornis agilis
Golden-crowned, see Basileuterus culicivorus
Golden-winged, see Vermivora chrysoptera
Hooded, see Wilsonia citrina
Kentucky, see Oporornis formosus
Kirtland's, see Dendroica kirtlandii
Lucy's, see Vermivora luciae
Orange-crowned, see Vermivora celata
Parula, see Parula americana
Prairie, see Dendroica discolor
Prothonotary, see Protonotaria citrea
Reed, see Acrocephalus scirpaceus
Tennessee, see Vermivora peregrina
Townsend's, see Dendroica townsendi
Wilson's, see Wilsonia pusilla
Worm-eating, see Helmitheros vermivorus
Yellow, see Dendroica petechia
Yellow-rumped, see Dendroica coronata
warbler, see Vermivora sp.
warblers, wood, 114–128
Ward, Richard M. P., see Orr, Craig, D., ———, Norman A. Williams, and R. G. B. Brown
Waterthrush, Louisiana, see Seiurus motacilla
Northern, see Seiurus noveboracensis
Waxwing, Cedar, see Bombycilla cedrorum
waxwings, see Bombycilla spp.
weasel, long-tailed, see Mustela frenata
Weaver, Cape, see Ploceus capensis
Weber, Michael J., Paul A. Vohs, Jr., and Lester D. Flake, Use of prairie wetlands by selected bird species in South Dakota, 550–554
Weick, Friedhelm, Birds of prey of the world, reviewed, 98–100
Weir, Ron D., see Edwards, Martin H., ———, and Robert B. Stewart
whale, pilot, see Globicephala macrorhynca
Whimbrel, see Numenius phaeopus
Whinchat, see Saxicola rubetra
Whip-poor-will, see caprimulgus vociferus
Whitacre, David, Devora Ukrain, and Gary Falxa, Notes on the hunting behavior and diet of the Crested Caracara in northeastern Chiapas and Tabasco, Mexico, 565–566
White-eye, Japanese, see Zosterops japonicus
Pale, see Zosterops pallida
white-eyes, see Zosteropidae
Whitlock, Ralph, Birds at risk. A compre-

hensive world-survey of threatened species, reviewed, 606–607
Whitmore, Robert C., see Seidel, George E. and ———
Whittow, G. Causey, see Pettit, Ned N., Gilbert S. Grant, and ———
Wiedenfeld, David A., A nest of the Pale-billed Antpitta (Grallaria carrikeri) with comparative remarks on antpitta nests, 580–582
———, see Robbins, Mark B. and ———
Wilde, Jonathan, see Rosenfield, Robert N. and ———
Willett, see Cataptrophorus semipalmatus
Williams, Morris D., see Schulenberg, Thomas S. and ———
Williams, Norman A., see Orr, Craig A., Richard M. P. Ward, ———, and R. G. B. Brown
Willis, Edwin O., The behavior of Scale-backed Antbirds, 447–462
Wilsonia canadensis, 491
  citrina, 25, 30, 74–79
  pusilla, 140, 352–353
Winn, H. E., see Burger, J., B. L. Olla and ———
wintering
  Myadestes townsendi, 297–302
  species at Monteverde, Costa Rica, 350–354
Wood, D. Scott, review by, 237
Woodcreeper, Plain-brown, see Dendrocincla fuliginosa
  Red-billed, see Hylexetastes perrotti
  White-chinned, see Dendrocincla merula
Woodpecker, Acorn, see Melanerpes formicivorus
  Downy, see Picoides pubescens
  Gila, see Centurus uropygialis
  Ladder-backed, see Picoides scalaris
  Pileated, see Dryocopus pileatus
  Red-bellied, see Melanerpes carolinus
  Red-cockaded, see Picoides borealis
  Red-necked, see Campephilus rubricollis
  Rufous-headed, see Celeus spectabilis
  Rufous-winged, see Piculus simplex
  Three-toed, see Picoides tridactylus
woodpeckers, see Picidae
woodswallows, see Artamus spp.
Woolfenden, Glen E., see Bancroft, G. Thomas and ———
Worthen, Gary L., see Gessaman, James A. and ———
Wren, Buff-breasted, see Thyrothorus leucotis
  Cactus, see Campylorhynchus brunneicapillus
  Carolina, see Thryothorus ludovicianus
  Clarión Island, see Troglodytes tanneri
  Fawn-breasted, see Thryothorus guarayanus
  House, see Troglodytes aedon
  Marsh, see Cistothorus palustris
  Rock, see Salpinctes obsoletus exsul
  Sedge, see Cristothorus platensis
  Socorro, see Thryomanes sissonii
Wyllie, Ian, The cuckoo, reviewed, 233–235
Xanthocephalus xanthocephalus, 265, 550–554, 585–590
Xema sabini, 10
Xenops, Plain, see Xenops minutus
  Rufous-tailed, see Xenops milleri
Xenops milleri, 479, 481–482
  minutus, 481
Yahner, Richard H., Avian nest densities and nest-site selection in farmstead shelterbelts, 156–175
Yellowlegs, Greater, see Tringa melanoleucus
  Lesser, see Tringa flavipes
Yellowthroat, Common, see Geothlypis trichas
Zammuto, Richard M. and Douglas James, Relationships of environmental factors to onset of autumn morning vocalizations in an Ozark community, 74–79
Zegers, David A., see Reed, J. Michael, Herbert E. Hays, and ———
Zenaida asiatica, 546–550
  aurita, 29
  graysoni, 8, 11, 16, 17
  macroura, 10, 17, 156–175, 185–197, 210, 546–550, 582–584
  macroura clarionensis, 10
  macroura marginella, 10
Zonotrichia albicollis, 74–79, 114–128, 140

zoogeography
  Penelope albipennis, 241–259
Zosteropidae, 114–128
Zosterops japonicus, 463–476
  pallida, 114–128
Zusi, Richard L., see Bentz, Gregory Dean and ———

This issue of *The Wilson Bulletin* was published on 31 January 1983.

7070 065

The Wilson Bulletin

Editor Jon C. Barlow

Department of Ornithology
Royal Ontario Museum
100 Queen's Park
Toronto, Ontario, Canada M5S 2C6

Associate Editor Margaret L. May

Assistant Editors Keith L. Bildstein
Gary Bortolotti
Nancy Flood

Senior Editorial Assistants Janet T. Mannone, Richard R. Snell

Editorial Assistants C. Davison Ankney
Peter M. Fetterolf
James D. Rising

Review Editor Robert Raikow
Department of Biological Sciences
University of Pittsburgh
Pittsburgh, PA 15260

Color Plate Editor William A. Lunk
865 North Wagner Road
Ann Arbor, MI 48103

Suggestions to Authors

See Wilson Bulletin, 91:366, 1979 for more detailed "Suggestions to Authors." Manuscripts intended for publication in *The Wilson Bulletin* should be submitted in triplicate, neatly typewritten, double-spaced, with at least 3 cm margins, and on one side only of good quality white paper. Do not submit xerographic copies that are made on slick, heavy paper. Tables should be typed on separate sheets, and should be narrow and deep rather than wide and shallow. Follow the AOU Check-list (Fifth Edition, 1957) and the 32nd Supplement (Auk, 90:411–419, 1973), insofar as scientific names of U.S. and Canadian birds are concerned. Summaries of major papers should be brief but quotable. Where fewer than 5 papers are cited, the citations may be included in the text. All citations in "General Notes" should be included in the text. Follow carefully the style used in this issue in listing the literature cited; otherwise, follow the "CBE Style Manual" (1972, AIBS). Photographs for illustrations should have good contrast and be on gloss paper. Submit prints unmounted and attach to each a brief but adequate legend. Do not write heavily on the backs of photographs. Diagrams and line drawings should be in black ink and their lettering large enough to permit reduction. Original figures or photographs submitted must be smaller than 22 × 28 cm. Alterations in copy after the type has been set must be charged to the author.

Notice of Change of Address

If your address changes, notify the Society immediately. Send your complete new address to Ornithological Societies of North America, Cornell Laboratory of Ornithology, 159 Sapsucker Woods Rd , Ithaca, New York 14850.

The permanent mailing address of the Wilson Ornithological Society is: c/o The Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109. Persons having business with any of the officers may address them at their various addresses given on the back of the front cover, and all matters pertaining to the Bulletin should be sent directly to the Editor.

Membership Inquiries

Membership inquiries should be sent to Dr. Keith Bildstein, Department of Biology, Winthrop College, Rock Hill, South Carolina 29733.

CONTENTS

THE BIOLOGY OF *TORREORNIS INEXPECTATA* I. A COMPARISON OF VOCALIZATIONS IN *T. I. INEXPECTATA* AND *T. I. SIGMANI* — *Eugene S. Morton and Hiram J. Gonzalez Alonso* 433

THE BEHAVIOR OF SCALE-BACKED ANTBIRDS — *Edwin O. Willis* 447

CENSUSES AND BREEDING OBSERVATIONS OF THE BIRDS ON KOHALA MOUNTAIN, HAWAII — *Charles van Riper, III* 463

OBSERVATIONS OF SOME UNUSUAL RAINFOREST AND MARSH BIRDS IN SOUTHEASTERN PERU — *Theodore A. Parker, III* 477

MIGRATION AND SUMMER DISTRIBUTION OF LESSER SNOW GEESE IN INTERIOR KEEWATIN — *Peter L. McLaren and Margaret A. McLaren* 494

ECOLOGICAL SEPARATION OF GREBES AND COOTS: INTERFERENCE COMPETITION OR MICROHABITAT SELECTION? — *Thomas D. Nudds* 505

ROLE SPECIALIZATION IN THE PARENTAL AND TERRITORIAL BEHAVIOR OF THE KILLDEER — *John T. Mundahl* 515

BIOLOGY AND BEHAVIOR OF BREEDING PIPING PLOVERS — *Winifred E. Cairns* 531

GENERAL NOTES

COMPARISON OF VARIABLE CIRCULAR-PLOT AND SPOT-MAP METHODS IN DESERT RIPARIAN AND SCRUB HABITATS — *Robert C. Szaro and Martin D. Jakle* 546

USE OF PRAIRIE WETLANDS BY SELECTED BIRD SPECIES IN SOUTH DAKOTA — *Michael J. Weber, Paul A. Vohs, Jr., and Lester D. Flake* 550

SEXING SAW-WHET OWLS BY WING CHORD — *Helmut C. Mueller* 554

COMMENTS ON SEXING SAW-WHET OWLS BY WING CHORD — *Martin H. Edwards, Ron D. Weir, and Robert B. Stewart* 555

USE OF TWO HABITATS RELATED TO CHANGES IN PREY AVAILABILITY IN A POPULATION OF OSPREYS IN NORTHEASTERN NOVA SCOTIA — *Ian Jamieson, Norman R. Seymour, and Robert P. Bancroft* 557

NEST PROVISIONING BEHAVIOR BY A MALE NORTHERN HARRIER ON THE DEATH OF HIS MATE — *Steven P. Thompson and John E. Cornely* 564

NOTES ON THE HUNTING BEHAVIOR AND DIET OF THE CRESTED CARACARA IN NORTHEASTERN CHIAPAS AND TABASCO, MEXICO — *David Whitacre, Devora Ukrain, and Gary Falxa* 565

FLORIDA RED-SHOULDERED HAWK ROBS AMERICAN CROWS — *Lawrence Kilham* 566

FEEDING BEHAVIORS AND EFFICIENCIES OF COMMON AND FORSTER'S TERNS — *J. Michael Reed, Herbert E. Hays, and David A. Zegers* 567

CLUTCH-SIZE AND PREFLEDGING SURVIVAL IN RED-WINGED BLACKBIRDS AT WILLIAMSTOWN LAKE, NEW BRUNSWICK — *Michael D. Rigby* 569

GROWTH, DIET, AND MORTALITY OF NESTLING GREAT BLUE HERONS — *T. E. Quinney* 571

DOWNY WOODPECKER SEXES SELECT DIFFERENT CAVITY SITES: AN EXPERIMENT USING ARTIFICIAL SNAGS — *Thomas C. Grubb, Jr.* 577

A NEST OF THE PALE-BILLED ANTPITTA (*GRALLARIA CARRIKERI*) WITH COMPARATIVE REMARKS ON ANTPITTA NESTS — *David A. Wiedenfeld* 582

INTERSPECIFIC NEST USE BY ARIDLAND BIRDS — *Deborah M. Finch* 582

AN APPARENT INSTANCE OF COMMUNAL NESTING BY AMERICAN OYSTER CATCHERS — *Brian R. Chapman* 584

SONG SPARROW PAIR RAISE FOUR BROODS IN ONE YEAR — *James N. M. Smith* 584

POST-COPULATORY DISPLAY IN THE LARK BUNTING AND OTHER SPECIES — *Robert W. Nero* 585

RESPONSES OF BLACK-CAPPED CHICKADEES TO MIRRORS — *Ellen J. Censky and Millicent S. Ficken* 590

TOOL USE BY GREEN JAYS — *Douglas C. Gayou* 593

A FLIGHT-SONG DISPLAY OF WHITE-THROATED MANAKIN — *Thomas H. Davis* 594

NOTES ON THE AGONISTIC BEHAVIOR OF COMMON MURRES — *Shane P. Mahoney and William Threlfall* 595

RECORDS OF REDHEAD × CANVASBACK HYBRIDS — *G. M. Haramis* 599

HIGH MORTALITY OF CEDAR WAXWINGS ASSOCIATED WITH HIGHWAY PLANTINGS — *Robert C. Dowler and Gustav A. Swanson* 602

ORNITHOLOGICAL LITERATURE — 604

PROCEEDINGS OF THE SIXTY-THIRD ANNUAL MEETING — 612

INDEX — 624

ACME
BOOKBINDING CO., INC.
SEP 9 1983
100 CAMBRIDGE STREET
CHARLESTOWN, MASS.

MCZ ERNST MAYR LIBRARY
3 2044 118 616 127